THE

EVOLUTION OF THE LAND PLANTS [EMBRYOPHYTA]

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By

DOUGLAS HOUGHTON CAMPBELL



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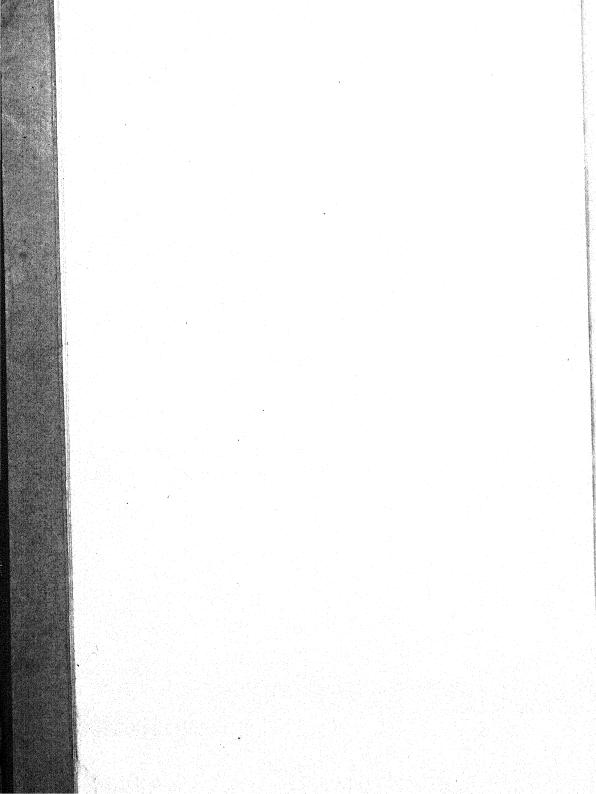
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To PROFESSOR F. O. BOWER



PREFACE

For many years the writer has devoted much time to a study of the development and relationships of the embryophytes, especially the archegoniates and lower angiosperms. In the present volume an attempt has been made to present the conclusions reached as to the origin and evolution of the main classes and orders of the Embryophyta.

Of course, these problems have engaged the attention of many botanists, and consequently many systems of classification have been proposed, but these are by no means always in accord.

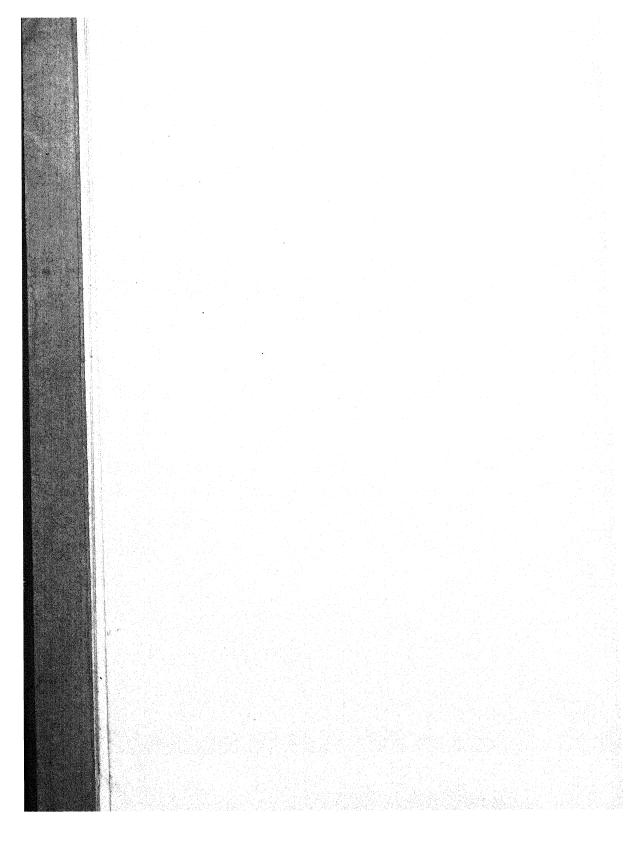
It is not expected that all of the conclusions presented by the writer will meet with general approval, but it is hoped they may direct attention to much-needed investigation of many disputed points in the classification of the embryophytes, which at present is in need of thorough revision.

Thanks are due Dr. Nathan van Patten for the preparation of the index.

DOUGLAS H. CAMPBELL

Stanford University October 1939

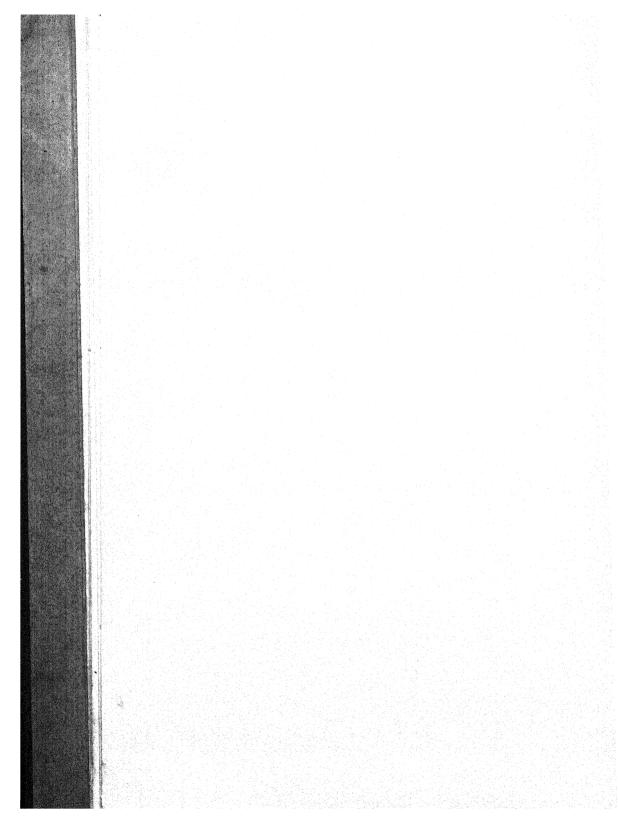




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THE EVOLUTION OF THE LAND PLANTS

(EMBRYOPHYTA)

CHAPTER I

INTRODUCTION

While the number of workers in the botanical field continues to increase, comparatively little has been done toward the establishment of a classification of the higher plants more in accord with our present knowledge than is the very antiquated system now in general use. Too often taxonomists are more interested in the discovery of new species and in questions of nomenclature than in a comprehensive study of the relationships of the larger groups.

With the opening of the twentieth century a new epoch was inaugurated in the history of plant evolution, the science of genetics. The two factors mainly responsible for the great interest in this subject were the remarkable experiments of Mendel, overlooked for some thirty years, and the "mutation theory" of DeVries. Immediately a host of investigators developed, botanists and zoölogists, the brilliant results of whose researches have added enormously to our knowledge of the factors concerned in evolution.

The present great vogue of genetics has attracted a large proportion of the botanists of the last generation, and while they have advanced greatly our knowledge of the mechanics of evolution, their absorption in the methods of evolution has diverted attention from some of the larger problems dealing with the history of the plant kingdom; and we must still depend largely upon a study of comparative morphology, ontogeny, and the fossil record for an understanding of the course of evolution in the higher plants.

With the continual accumulation of new data bearing on the history of the plant kingdom, it is desirable from time to time to examine how far these new discoveries require a modification of prevalent theories dealing with phylogeny. For example, it is very commonly held that the flowering plants—angiosperms—can all be traced back to a single ancestral type. There are very serious objections to this theory, as both the fossil record and comparative morphology make it more probable

that the angiosperms are "polyphyletic," i.e., that they comprise numerous parallel lines of development derived from several independent but allied forms. Thus the "family tree" is likely to prove a much-branched "shrub," with sundry outlying suckers spreading from its roots.

In comparing similar structures also the question of "homoplasy," i.e., the independent origin of such structures in unrelated or remotely related organisms must be considered. Such homoplastic structures, for example, are the "leaves" of mosses, certain algae, and those of the vascular plants. Sometimes it is hard to tell whether two structures are really "homologous," i.e., genetically connected, or are merely homoplastic.

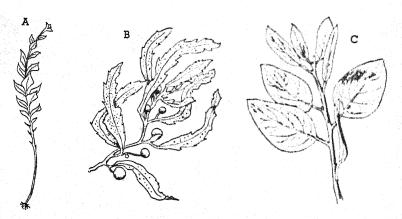


Fig. 1.—Homoplasy. Leaves in: A, a moss, Tetraphis; B, an alga, Sargassum; C, a seed-plant, manzanita (Arctostaphylos).

Owing to the relative simplicity of all plants as compared with animals, it is hardly possible to establish such definite major groups as are recognized in the animal kingdom. The structures of plants are far less specialized and their cells are correspondingly uniform. Where specialized tissues occur, like the skeletal structures, e.g., the woody tissues of the vascular plants, they are much less constant than those of animals, and moreover are often homoplastic—so that they are much less reliable as indicators of genetic relationship than is the case in animals. Moreover the complex plants are not individualized. An oak tree is not an individual in the sense that a dog is, but is rather a colony of potentially independent members.

Plants are, on the whole, far more conservative than animals, and most of the existing types can be traced back to a very remote period. Even existing genera, like Sequoia, Sassafras, and Populus, are found fossil at a period when the modern families of birds and mammals had not come into existence.

In attempting to trace relationships between any two groups of organisms it is among the simpler members that the closest resemblances are to be sought. Highly specialized forms, like the leafy mosses and the leptosporangiate ferns, probably represent the ends of divergent phyla, and have not given rise to any higher types. It must also be borne in mind that some of the most successful living plant types retain certain primitive characters. A notable case is that of the pollen sacs of the flowering plants, which differ but little from the sporangia of the primitive pteridophytes. A parallel case might be cited in the animal kingdom. The extremities of man, for example, are much more primitive in structure than the highly specialized limbs of a horse.

All plants below the mosses (bryophytes) are still treated in many current textbooks as forming a single primary division, or subkingdom, Thallophyta. Within this group are included plants ranging from microscopic, unicellular algae and bacteria, to massive fungi and giant seaweeds of very complex structure. That the inclusion, in a single subkingdom, of such a heterogeneous assemblage of evidently divergent types is decidedly unscientific, is sufficiently obvious.

On the other hand, the three groups of higher green plants—Bryophyta (mosses), Pteridophyta (ferns), and Spermatophyta (seed plants)—are treated as independent subkingdoms, co-ordinate with the whole of the Thallophyta, although it is generally recognized that these three groups are essentially similar in their reproduction. There is abundant reason for placing these three groups in a single subkingdom, Embryophyta, as is done by Engler.

While the term "Thallophyta" might be retained for convenience' sake, as the zoölogists still speak of "invertebrates," in neither case can this be assumed to imply a definite natural assemblage.

The embryophytes are the typical green land plants, and it is with these, their relationships among themselves, and with their nearest relatives among the algae, that the following pages are chiefly concerned.

The essential similarity in the reproduction of the embryophytes was demonstrated nearly eighty years ago by the distinguished German botanist, Hofmeister, whose researches in the morphology and embryology of these plants mark an epoch in the history of botany. In spite of the confirmation and extension of Hofmeister's conclusions by many later investigators, the old classification still holds its own—which might be interpreted to indicate that the majority of botanists are, to say the least, inclined to be conservative.

Hofmeister's work has been the inspiration for an immense volume of later investigations dealing with the comparative morphology of the embryophytes, and these investigations furnish a basis for a more satisfactory classification, although, of course, any classification proposed, must, for the present, be recognized as more or less tentative. Since Hofmeister's day much has been done to advance our knowledge of the fossil embryophytes; but these investigations are restricted mainly to the so-called "vascular" plants, and very little is known of the geological history of the simpler forms, like the liverworts and mosses. The life cycle of all embryophytes shows two marked phases, sexual and nonsexual. This "alternation of generations," while common to all embryophytes, is most conspicuous in the lower members, the "archegoniates." In these the sexual plant, the "gametophyte," the sexual reproductive organs. archegonium and antheridium, develop the sex cells-"gametes," eggs or sperms. The male gametes, spermatozoids, are ciliated and actively motile. The gametophyte may attain a relatively large size in some of the larger liverworts and mosses; but in the vascular plants, pteridophytes and spermatophytes, it is much less conspicuous and finally in the flowering plants is so greatly reduced in size as to be generally quite overlooked.

The male gametes in the bryophytes and pteridophytes are minute, ciliated bodies, closely resembling the spermatozoids of the green algae, and, like these, require free water in order to function. The ripe antheridium, when water is applied, discharges the sperm cells containing the spermatozoids, which escape and swim to the ripe archegonium, which also opens when wet and permits the entrance of the spermatozoids, one

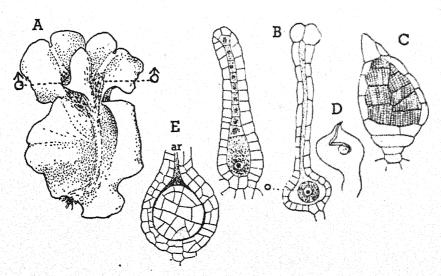


Fig. 2.—A, gametophyte of a liverwort, Calycularia; the d'antheridia; B, archegonia of a liverwort, Riccia; C, antheridium of the same; D, a spermatozoid; E, the embryo-sporophyte of Riccia within the archegonium.

of which penetrates the egg cell and effects its fertilization. The necessity of free water for effecting fertilization suggests that the gametophyte has arisen from some aquatic ancestral forms.

As a result of the fusion of the two sexual nuclei, the nucleus of the fertilized egg cell or zygote is "diploid," i.e., has twice the number of chromosomes of the "haploid" nuclei of the cells of the gametophyte. The zygote begins to grow and develops into a multicellular body, the embryo. all of whose cells have diploid nuclei. The embryo is retained for a longer or shorter time within the archegonium whose outer tissues form a protective envelope about it. The embryo develops into a more or less complex body which ruptures the archegonial tissues and becomes the "sporophyte," so-called from the characteristic tetrads of spores produced by the division of special "spore mother cells." The first nuclear [division in the mother cell is a "reduction division"—"meiosis"—and the four spores resulting from the second division have the haploid chromosome number. Spore formation is thus an asexual process, and the sporophyte is strictly an asexual or neutral organism. The spores on germination give rise to the haploid gametophyte upon which the sexual organs are developed.

That the embryophytes are descended from aquatic ancestors is generally admitted, but there is much difference of opinion as to how their present terrestrial habit has been developed.

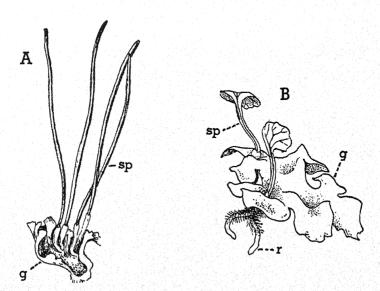


Fig. 3.—A, gametophyte, g, of a liverwort, Anthoceros, bearing four sporophytes, sp; B, gametophyte of a fern, Danaea, with two young sporophytes; r, root.



The principal classes of the algae, viz., green algae (Chlorophyceae), red algae (Rhodophyceae), and brown algae (Phaeophyceae), probably constitute entirely independent phyla. Moreover, from the most recent investigations on the green algae it seems quite likely that within this class are a number of independent lines of evolution which may be traced back to separate unicellular types.

The green algae are predominantly fresh-water organisms, and presumably older types than the brown and red algae, which are mainly salt-water plants whose peculiarities are largely associated with their marine environment. It is extremely unlikely that these highly specialized seaweeds have given rise to the terrestrial embryophytes, which both structurally and physiologically are much more akin to the fresh-water green algae.

While the vegetative structure of certain green algae and the lower embryophytes are sufficiently alike, the differences in their reproductive organs and the sporophyte are very great, and it must be admitted that there is a great gap between the existing green algae and any known embryophyte.

How and when the algal ancestors of the embryophytes first took to

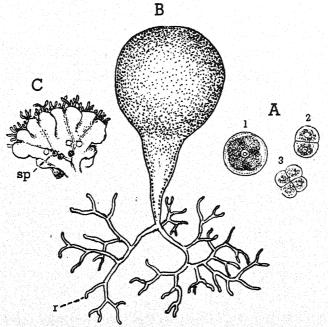


Fig. 4.—A, a unicellular alga, *Protococcus*, showing cell division; B, a terrestrial green alga, *Botrydium*, showing much-branched roots (rhizoids); C, *Riccia natans*, an amphibious liverwort; sp, the simple sporophytes.

the land is of course purely conjectural. There are many seaweeds which are regularly exposed to the air at low tide; but this exposure is temporary, and it is hardly likely that these essentially salt-water organisms have any relationship with any existing land plants, which have much more in common with some of the fresh-water green algae.

The migration of the algal ancestors of first true terrestrial plants from their typical aquatic habitat to life on land was probably a very gradual one. There are still some simple green algae adapted to terrestrial life. The unicellular *Protococcus*, for example, vegetates so long as the air is sufficiently moist, becoming dormant when moisture is lacking. A more striking instance is the curious little alga, *Botrydium*. This grows upon damp soil, the exposed portion forming a dark green vesicle, while penetrating the soil is an extensively branched root system, which enables it to live for a considerable time as a land plant, since the loss of water by evaporation is made good so long as sufficient moisture remains in the soil.

It is quite conceivable that some more highly developed multicellular green alga might similarly develop roots (rhizoids) attaching it to the mud left by the evaporation of the water in which it was growing, thus prolonging the growth for a longer or shorter time. It would have to return to the aquatic condition, however, in order to insure fertilization of the egg by the ciliated spermatozoids. Such an alga might be described as "amphibious," and a similar condition occurs in some of the lower archegoniates. The often cited liverwort, *Riccia natans*, has very much the same history, as it is a true aquatic as a rule but may later settle on the mud, where it grows more vigorously than in the floating condition, and has been described as a distinct species. Some such procedure on the part of the assumed ancestral algae may have been the starting point for the future hosts of land plants. All but the highest of these, the seed plants, retain evidences of their aquatic origin.

The uniform conditions of their environment have tended to great conservatism in many fresh-water organisms like the simpler green algae and Protozoa, which probably have come down but little altered from the remotest antiquity. Once established on land, however, the environment is immensely more varied and the scope for the evolution of new forms correspondingly increased.

In changing from the aquatic to the terrestrial condition, the water supply, of course, is of primary importance, not only the absorption through roots, or other organs, but also its conservation by protecting the exposed surfaces against evaporation by a more or less effective waterproof layer of cells.

An alga floating in the water is supported on all sides; but removed

from the water it collapses, owing to the absence of supporting or "mechanical" tissues, which are necessary if a plant is to maintain an upright position in the air. Among the lower embryophytes are many examples of plants which have retained this primitive type of gametophyte and, like the algae, are deficient in the development of these mechanical tissues and thus lie prostrate, as it may be assumed was the case with their algal prototypes. Among such forms are many liverworts. The gametophytes of the ferns also resemble these simple liverworts. This prostrate condition, while doing away with the necessity of skeletal tissues, has the advantages of exposing a smaller surface to the air and thus reducing the loss of water through evaporation and at the same time affording a larger area for the attachment of roots for absorbing water from the soil.

In the more specialized liverworts and mosses the gametophyte is a leafy shoot which, especially in the mosses, often shows a fairly complete system of skeletal and water-conducting tissues, enabling the shoot to assume an upright position.

In a recent paper¹ there is announced the discovery, in the Upper Cambrian of Sweden, of spores recalling those of the existing embryophytes. These spores show the trifid scars characteristic of the spore tetrads of the living liverworts and ferns. It is not unlikely that these spores belonged to some amphibious plant intermediate between the green algae and the archegoniates.

¹ W. C. Darrah, "Spores of Cambrian Plants," Science, 86: August 1937.

CHAPTER II

CLASSIFICATION OF THE EMBRYOPHYTA

That the classification of the embryophytes is at the present time far from satisfactory is beyond question; and although many investigations in recent years have added much to our understanding of the interrelationships of the major groups, much more information is essential before anything approaching a definitive system can be established. Any system, therefore, based upon our present knowledge, must be at best tentative.

Especially important have been the discoveries in the fossil field which have shed much light on the early history of the vascular plants. Relatively little, however, is known regarding the geological history of the bryophytes, of which few recognizable fossil remains have been found.

Existing plants evidently represent fragments of many lines of development whose relationships to each other are often obscure. Even where marked resemblances exist between certain forms, there is always the possibility that such resemblances have arisen independently from similar but not identical ancestors, i.e., are homoplastic rather than homologous.

Three categories of embryophytes are generally recognized: Bryophyta (mosses), Pteridophyta (ferns), and Spermatophyta (seed plants). That within each of these groups there are numerous phyla whose relationships are, to say the least, doubtful, becomes more and more evident as the geological history, as well as the ontogeny, of the embryophytes become better known. Nevertheless they all agree in the essential similarity of their reproduction, and the production of a multicellular embryo, as the result of fertilization instead of the unicellular zygote—usually a resting spore—characteristic of the green algae. The organism developed from the embryo sooner or later produces by cell division numerous spores and is the sporophyte.

This similarity in the life history of all the embryophytes indicates an origin from similar, if not identical, algal ancestors, and, for the present at least, warrants their inclusion in a single primary division or subkingdom.

The life history of the embryophytes is most clearly seen in some of the less specialized types, and may be briefly summarized.

From the germinating spore the gametophyte develops. It may be a simple prostrate thallus, comparable to such algae as *Ulva* or *Coleochaeta*; or it may become a relatively large leafy plant of considerable complex-

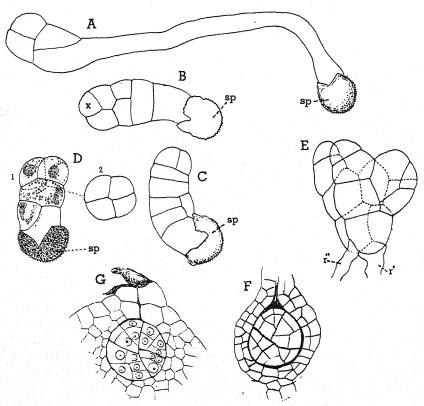


Fig. 5.—A-E, development of the young gametophyte of a liverwort, Anthoceros; sp, the spore membrane; r', r'', the first rhizoids; F, young embryo of Riccia; G, embryo of a fern, Onoclea, enclosed in the archegonium.

ity, as in some leafy liverworts and especially the true mosses. The gametophyte bears the sex organs, archegonia and antheridia.

From the fertilized egg, within the archegonium, by continuous growth and specialization is developed the sporophyte, whose primary function is spore production but which ultimately may become the predominant phase in the life history of the plant. This is the case in the "vascular" plants, viz., pteridophytes and spermatophytes.

While for convenience' sake the terms bryophyte, pteridophyte, and spermatophyte may be retained, it is very evident that within each of these categories several quite independent lines have arisen. Thus the fossil record shows that seeds have developed in many entirely unrelated phyla. It is therefore clear that the prevalent classification of the embryophytes is not an entirely natural one and is much in need of revision.

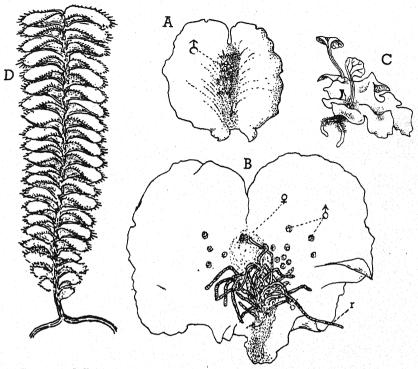


Fig. 6.—A, thallose gametophyte of a liverwort, Calycularia; \mathcal{C} , antheridia; B, gametophyte of a fern, Gleichenia, bearing archegonia, \mathcal{C} , and antheridia, \mathcal{C} ; C, gametophyte of a fern, Danaea, bearing two young sporophytes; D, a liverwort, Plagiochila, having definite leaves.

The Bryophyta (Muscineae) include the three classes Anthocerotes, Hepaticae, and Musci. All of these, so far as is known, agree in having minute biciliate spermatozoids, in which respect they agree with the majority of the green algae (Chlorophyceae); and this is one argument for the theory that they have been derived from the latter. Among the Chlorophyceae the order Ulothricales, both in cell structure and in some features of the reproduction, approaches most nearly the lower embryophytes. The cell in the Ulothricales usually has a single large green chromatophore which contains one or more characteristic bodies-pyrenoids. In most embryophytes the green cells usually contain numerous small chromatophores; but in the Anthocerotes there is usually but a single large chromatophore, very much like that of the Ulothricales and also in many cases having a distinct pyrenoid. In one genus of the Anthocerotaceae, however, Megaceros, the cells contain several chromatophores, and in this respect is intermediate between the typical Anthocerotaceae and the higher embryophytes.

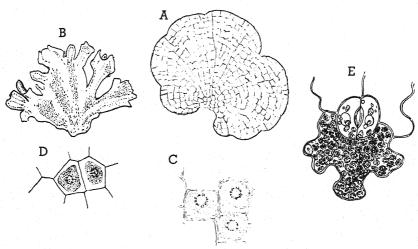


Fig. 7.—A, gametophyte of a green alga, Coleochaete scutata; B, a liverwort, Notothylas; C, cells of Coleochaete, showing the solitary chloroplast and pyrenoid; D, cells from a liverwort, Megaceros, with similar chloroplasts; E, epidermal cells from a fern leaf, showing numerous chloroplasts.

In nearly all of the embryophytes except the higher seed plants the archegonium is very similar, and these are sometimes known as the Archegoniatae.

The second series of the embryophytes, the pteridophytes, have left abundant fossil remains, and their early history is much better known than that of the bryophytes. Four classes of these exist today, viz., Psilophytineae, Lycopodineae, Equisetineae, and Filicineae.

At the present time the Filicineae (ferns) greatly outnumber all the other pteridophytes. The Psilophytineae have only two living genera, with very few species; the Equisetineae have a single genus, Equisetum, with about twenty-five species; and the Lycopodineae have two families with two large genera, Lycopodium and Selaginella. All of these are represented by many types from the Devonian to the present. The Lycopodineae (club mosses) differ from the three other classes in one very important character: they have small biciliate spermatozoids which resemble those of the typical bryophytes and possibly indicate a more or less direct relationship with the latter. The other three classes have large multiciliate spermatozoids whose nearest counterpart among the algae is found in a few forms like Oedogonium. It is possible that this multiciliate condition is secondary and has been derived from the biciliate type. This difference is a very important one and has been used as a basis for the separation of the pteridophytes into two primary divisions—Biciliatae and Polyciliatae.

THE ARCHEGONIUM

The archegonium of the liverworts (Hepaticae) and mosses is a flask-shaped organ containing the egg cell. The neck consists usually of five or six peripheral rows of cells with an axial row whose lowest member is the egg, which occupies the enlarged base or "venter" of the archegonium.

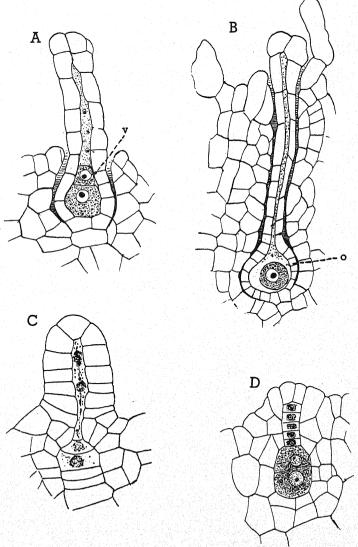


Fig. 8.—The archegonium. A-B, a liverwort, Riccia; C, a fern, Botrychium; D, Notothylas (Anthocerotaceae).

When ripe, the cell walls of the axial cells become mucilaginous and the contents disorganized, so that when water is absorbed the swelling of the mucilaginous axial cells together with the pressure of the turgid neck cells ruptures the apex of the archegonium and discharges the remains of the canal cells, leaving an open canal leading to the egg. The spermatozoids enter the canal and reach the ventral cavity.

In the Anthocerotes and pteridophytes the base of the archegonium is fused with the adjacent tissues and there are differences in the structure of the neck which in the ferns (Filicineae) and horse-tails (Equisetineae) has but four rows of peripheral cells and usually but two neck canal cells. Among the club mosses some species of *Lycopodium* show a remarkable increase in the number of cells in the archegonium neck, both outer cells and canal cells, in both respects resembling the mosses.

ANTHERIDIUM

Much greater differences are found in the antheridium, which usually is formed from a single superficial cell and in most bryophytes is a capsule borne on a stalk. The capsule consists of a single parietal cell layer and a central mass of cells, each containing a single biciliate spermatozoid. The least specialized antheridia are found in the more primitive pteridophytes. In these the antheridium consists of a mass of sperm cells (spermatocytes) embedded in the gametophyte and covered with a single layer of superficial cells. The major part of the spermatozoid, which is more or less elongated and spirally twisted, is composed of the nucleus of the spermatocyte. Associated with the nucleus is a peculiar body, the "blepharoplast," from which the cilia arise.

In certain ferns it has been shown that the spermatozoid penetrates the nucleus of the egg cell and the chromosomes gradually separate and mingle with those of the egg nucleus but do not fuse with them. This fusion nucleus thus has the diploid chromosome number which is passed on to the cells of the embryo developed from the zygote, and this diploid character persists in the cells of the sporophyte until the first division of the cells from which the spore tetrads are formed.

The zygote, immediately after fertilization, develops a cell wall; but instead of assuming the resting state, characteristic of most green algae, it increases in size and undergoes repeated cell division, thus forming the multicellular "embryo." Sooner or later definite sporogenous tissue is formed. Except in a few cases, e.g., the "embryo sac" of some of the flowering plants, each "spore mother cell" produces a tetrad of spores. The first nuclear division in the diploid mother cell is a "reduction division"—meiosis—so that after the second division, the four resulting spores have the haploid chromosome number of the gametes and this is

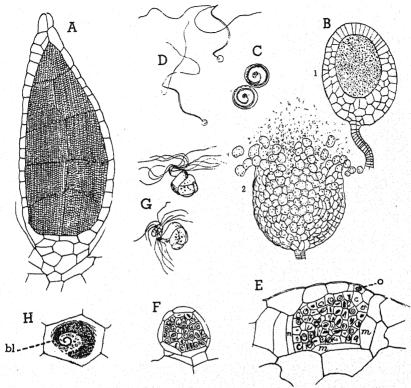


Fig. 9.—Antheridium. A, antheridium of a liverwort, Fimbriaria; B, of a foliose liverwort, Porella; C, spermatocytes; D, spermatozoids of Porella; E-F, antheridia of ferns, E, Angiopteris; F, Osmunda; G, spermatozoids of Osmunda Claytoniana; H, spermatocyte of Ophioglossum pendulum; bl, blepharoplast.

transferred to the new generation of gametophytes developed from the germinating spores.

In the bryophytes the sporophyte always remains to a certain extent dependent upon the gametophyte—in a sense a parasite, although, as in many of the mosses, it may be highly specialized and to a certain extent self-supporting. In the pteridophytes, however, the sporophyte finally becomes an independent plant, developing leaves and roots and special spore-producing organs—sporangia. The sporophyte may attain large size, as in the tree ferns and some of the large species of Equisetum and Lycopodium. With the growing importance of the sporophyte in the pteridophytes the gametophyte becomes relatively inconspicuous and in some cases is reduced to very minute proportions. This is seen in the "heterosporous" forms, where it is almost microscopic and composed of only a few cells. In all cases, however, there are developed typical arche-

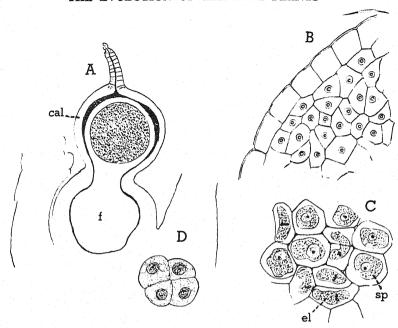


Fig. 10.—A, embryo of a liverwort, Targionia, enclosed in the enlarged venter (cal, calyptra) of the archegonium; the sporogenous tissue (archesporium) is shaded; f, the foot; B, highly magnified portion of the capsule, showing the unistratose capsule wall, and the archesporial tissue; C, beginning of differentiation of the archesporium into (sp) spore mother cells, and (el) elaters; D, young spore tetrad.

gonia and antheridia, and fertilization is effected by free-swimming, ciliated spermatozoids as in the bryophytes.

In the highest embryophytes, the spermatophytes, or seed plants, the gametophytes may be reduced to microscopic size and with very few exceptions the male gametes are no longer motile. The spermatophytes are heterosporous, i.e., there are two sorts of spores, microspores and megaspores. The former (pollen spores) produce a very rudimentary male gametophyte which forms a long "pollen tube" by which the male nuclei are conveyed to the egg. The megaspore never becomes free and is enclosed permanently in the sporangium (ovule). In the more primitive seed plants, e.g., cycads and conifers, the female gametophyte (embryo sac) developed within the megaspore may attain considerable size and bear archegonia much like those of the pteridophytes. In the higher flowering plants there is some question whether the embryo sac can always be considered as the exact equivalent of a megaspore, and the extremely reduced gametophyte which does not develop a definite archegonium is completely parasitic upon the tissues of the sporophyte which surround it. The flowering plant, therefore, as usually understood, is the sporophyte, or nonsexual phase, whose sexual stage is reduced to the very rudimentary gametophytes developed from the germinating pollen spore and embryo sac. Water is no longer necessary for the transport of the male gametes, and the last trace of their aquatic ancestry has disappeared.

While most of the fossil embryophytes show more or less evident affinity with living types, there are certain groups, especially among the most ancient forms, whose relationships are by no means clear and whose classification is still doubtful. Examples of these are the Rhyniaceae, Cordaitales, Caytoniales, and Pteridospermeae, concerning which there is much diversity of opinion.

ALTERNATION OF GENERATIONS

The origin and significance of the phenomenon of alternation of generations as it occurs in the embryophytes, and its bearing upon the origin of the independent sporophyte of the higher plants has been the subject of much controversy.

While the phenomenon occurs in the marine red and brown algae, it has evidently developed independently in these classes; but such structures as the complicated sporocarps found in many of the former class are not in any proper sense homologous with the sporophyte of a moss or fern, and it is among the much simpler fresh-water green algae that we must look for the nearest relations of the archegoniates. Of the green algae, as has already been indicated, the Ulothricales most nearly suggest what may have been the progenitors of the first embryophytes.

The origin of the sporophyte is to be sought in the zygote of some such algae. This in its simplest condition is a single thick-walled resting e-9 spore, adapted to resist drought and changes of temperature fatal to the growing plant. It is primarily the terrestrial phase of these typically aquatic organisms. The diploid resting spore on germination gives rise to a number of free-swimming haploid spores (zoöspores), which produce a new generation of sexual plants. The first division in the germinating spore is a reduction division and restores the haploid chromosome number to the zoöspores.

In Coleochaete, the most specialized member of the Ulothricales, there is a significant advance in the development of the zygote. Before reaching its resting stage the zygote grows to several times its original size. There is a repeated division of the original chromatophore, but the ripe zygote still has but a single nucleus. On germination the zygote gives rise to a globular mass of cellular tissue which recalls the embryo-sporophyte of Riccia, the simplest sporophyte known among the embryophytes. However, in Coleochaete the first nuclear division in the germinating zygote is a reduction division, as it is in the other Ulothricales, and all the

e.g. oedogoni

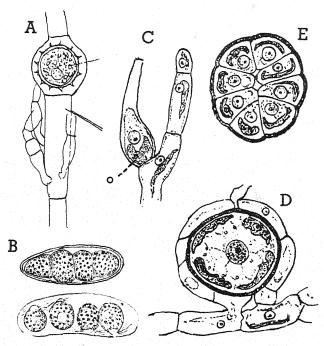


Fig. 11.—A, a green alga, Oedogonium, showing the resting spore (zygote) within the oögonium; B, germination of the zygote of Oedogonium, showing the four free zoöspores (after Pringsheim); C-E, Coleochaete pulvinata; C, the oögonium; D, zygote surrounded by sterile cells; E, germination of zygote into an embryo-like mass of cells (C-E, after Oltmanns).

subsequent cells are haploid; while in *Riccia* the diploid condition persists until the first division in the spore mother cells. Physiologically the spores replace the single resting spore of the algae.

While the globular cellular body developed from the zygote of Coleochaete cannot be strictly homologized with the embryo of Riccia, it is nevertheless a step in the direction of a true sporophyte and results in a notable increase in the spore output compared with the other green algae. These, being fresh-water organisms, are subject to drying up, and the resting spores, developed at the end of the active growing period, are an obvious adaptation for surviving a period of desiccation. The lower embryophytes may be considered as amphibious. The gametophyte requires free water in order that fertilization may be effected; but the sporophyte, the descendant of the zygote, is essentially a terrestrial organism—and in the course of evolution, as the terrestrial habit becomes more pronounced, it has played a more and more important role in the history of the embryophytes, with a corresponding reduction in the structure of the gametophyte.

There are two opposing views as to the nature of the alternation of

generations. The "antithetic" theory holds that the sporophyte is essentially a neutral (asexual) organism derived from a progressive elaboration of the zygote of some algal ancestors and is interpolated in the life history of the gametophyte, or sexual generation. The writer believes that this theory is strongly supported by the evidence of both comparative morphology and ontogeny, and this theory will be adopted in the discussion of the evolution of the embryophytes presented in the following pages.

Opposed to the antithetic theory is the "homologous" theory, which holds that the sporophyte is a modification of the gametophyte and is not a new structural type. There are undoubtedly some strong arguments for this view—the most important being the phenomena of "apospory" and "apogamy," i.e., the origin of the sporophyte by vegetative budding from the gametophyte and vice versa. As most, at least, of the observed cases of apogamy and apospory are the result of abnormal conditions and the other arguments are mostly purely speculative, with no concrete evidence, it seems to the writer that the evidence for homologous alternation is much less convincing than that for antithetic alternation.

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CHAPTER III

THE GAMETOPHYTE

As already indicated, the nearest relatives of the lower archegoniates are to be sought among the Chlorophyceae, and of these the Ulothricales show the closest resemblances. The Ulothricales are for the most part simple fresh-water algae, although some of them, like *Ulva*, are seaweeds. The majority are filamentous, i.e., composed of single cell rows; but there are also thallose forms like *Ulva* and *Coleochwete*. These thallose algae might be compared with some of the simplest liverworts, but it is hardly likely that there is any direct relationship between them and any existing types.

A characteristic of the Ulothricales is the single chromatophore (chloroplast) in each cell. Embedded in the chromatophore is a peculiar body (sometimes more than one), the "pyrenoid." Among the archegoniates, pyrenoids have been found only in the Anthocerotes, where as a rule also there is a single chromatophore in each cell.

The Anthocerotes, perhaps, represent the most primitive type of gametophyte among the existing archegoniates. In its simplest form it is a prostrate flat thallus composed of almost uniform cells and attached to the substratum by simple unicellular roots (rhizoids). The cells are very much like those of Coleochaete, for example, and in many species the single flat chromatophore has a conspicuous pyrenoid, although this cannot always be demonstrated. While as a rule there is but a single chromatophore, there are some exceptions. Thus in Anthoceros Pearsoni two chromatophores are often found, and in Megaceros there may be as many as a dozen in the larger cells. In the latter case the pyrenoid appears to be absent and the cell structure resembles that of the higher archegoniates. Perhaps in the Anthocerotes we see the gradual elimination of this characteristic algal organ and a transition to the condition found in the Hepaticae.

Aside from the Anthocerotes the most primitive of the archegoniates are the Hepaticae, or liverworts, in a restricted sense. In the less specialized Hepaticae, e.g., Aneura, Pellia, the gametophyte is very similar to that of the Anthocerotes. Like these the flat prostrate thallus is composed of uniform tissue and provided with unicellular rhizoids. The growth of the thallus is from a definite apical cell. The gametophyte may branch either dichotomously by a forking of the apex, or by the formation of

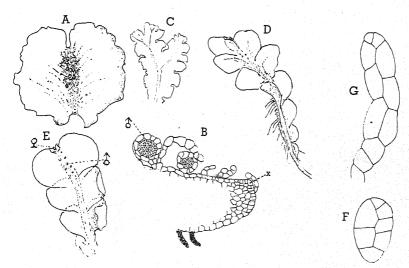


Fig. 12.—Gametophytes of liverworts, Jungermanniales. A, male plant of Calycularia; B, section of antheridial receptacle; C, Blasia; D, E, Noteroclada (Androcryphia); F, young gametophyte of Pellia calycina; G, young gametophyte of Aneura palmata (F, G, after Leitgeb).

lateral branches. More commonly there is a tendency to develop an axial thicker region, which finally becomes a definite midrib, e.g., *Metzgeria*, *Pallavicinia*, *Podomitrium*. In these forms, except for the thickened midrib, the thallus is composed of a single layer of cells (is "unistratose"). The inner cells of the midrib may be greatly elongated, with thickened cell walls suggesting the water-conducting tissues of the "vascular" plants, and probably serving the same purpose.

This specialization is still more marked in such forms as *Umbraculum* and some species of *Pallavicinia*. In these there is a prostrate "rhizome," in which the lamina is quite suppressed. From this rhizome arise vertical shoots which grow upward, and the aper forks repeatedly, the branches thus formed developing a thin lamina and midrib so that the flat dichotomous branch system resembles a small fern leaf and constitutes a definite photosynthetic organ.

In several families of Hepaticae definite simple leaves are found—and it is evident that these organs have had an independent origin in several unrelated groups. The tendency to develop marginal leaf-like lobes occurs in various genera of the "Anacrogynae," e.g., Fossombronia, Pallavicinia, Symphyogyna. In more advanced types, like Treubia, these lobes assume a definite leaf-like form and arise in regular sequence from the segments of the apical cell. From some such forms there have presumably arisen the predominant "foliose" or "leafy" liverworts, the "Acrogynae," which greatly outnumber all the other Hepaticae.

The course of evolution has been very different in the very characteristic order of Hepaticae, the Marchantiales. In these the strictly thallose form has been retained, but there has been a notable specialization of the tissues. In the simplest type, Riccia, the lower (ventral) region is composed of compact tissue without intercellular spaces, while the upper (dorsal) region is composed of chlorophyllous spongy tissue, with irregular intercellular spaces opening at the upper surface of the thallus but without any definite pores. This spongy green tissue forms an effective photosynthetic system.

In the more specialized Marchantiales there is a definite epidermis with pores analogous to the stomata of the higher plants, and sometimes the cells surrounding the pore can act in a manner comparable to the guard cells of the typical stomata.

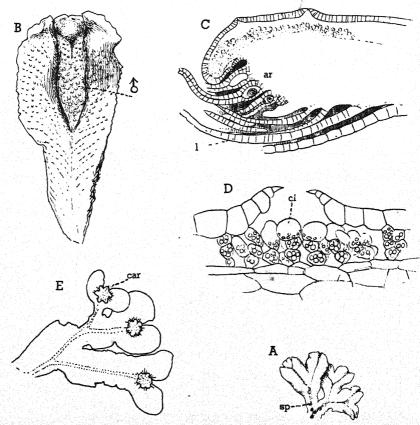


Fig. 13.—Liverworts, Marchantiales. A, Riccia glauca; B, male gametophyte of Fimbriaria Californica; C, apex of female shoot of Targionia; D, air-chamber of Targionia; cl, chlorophyllous cells; E, female plant of Dumortiera trichocephala; car., carpocephala.

In Riccia, the sex organs are borne singly on the dorsal surface of the gametophyte, but in most of the Marchantiales they are segregated in definite areas—and may be borne upon greatly modified special shoots.

On germination, the spores of the Hepaticae may first develop a filamentous "protonema" before the thallose condition is attained; but this is not always the case, and only in exceptional cases is a protonema produced comparable to that in the true mosses.

In the latter, the Musci, there is developed a protonema, usually filamentous in form and extensively branched. In the peat mosses, Sphagnaceae, regarded as the most primitive of the mosses, it is thallose and suggestive of the liverworts. From this protonema, as a bud, the definitive gametophyte is developed. In the mosses the gametophyte of the archegoniates reaches its most perfect development.

The adult gametophyte is a leafy plant, often upright, with a defi-

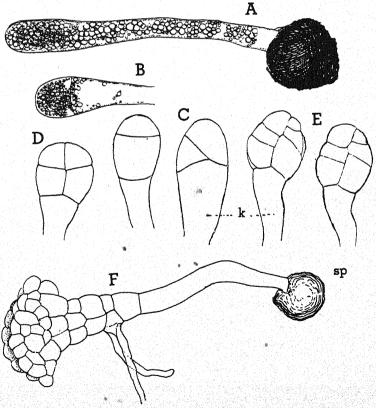


Fig. 14.—A-E, germination stages in Riccia trichocarpa; k, protonema; F, young gameto-phyte of Fimbriaria Californica.

nite axis bearing conspicuous, sometimes highly specialized leaves. This leafy shoot bears the archegonia or antheridia and might be denominated the gametophore. While the alga-like protonema originally comes from the germinating spore, it may arise secondarily by branching from the primary protonema or even from the leafy gametophore.

The thallose protonema of *Sphagnum* may indicate that the latter is in a way intermediate between the higher mosses and some liverwort-like ancestors—possibly Anthocerotes. At any rate, the evidence indicates a derivation of the mosses from forms with a thallose protonema from which secondarily the alga-like protonema has been derived.

Like the acrogynous Hepaticae, the leafy shoot of the mosses grows from a single tetrahedral apical cell, from whose segments the leaves arise. The leaves, also, in most mosses show a definite apical growth. Unlike the leafy liverworts, whose tissues are very uniform, the tissues of the higher mosses show a degree of differentiation comparable with that of the sporophyte of the vascular plants. The leafy shoot of some of the mosses may reach a height of a foot or more. Dawsonia superbar from Australia and New Zealand is sometimes 40–50 centimeters in height with leaves 2 centimeters in length, and has an elaborate conductive system very much like that of the higher plants. Dawsonia may be said to represent the extreme limit in specialization that the gameto-phyte has been able to reach.

PTERIDOPHYTA

While the gametophyte of the pteridophytes shows a marked range in size and structure, it never attains either the dimensions or the specialization found in the higher liverworts and mosses. Among the ferns (Filicineae), which are the most numerous of the eixsting pteridophytes, the gametophyte resembles that of the more primitive Hepaticae and in some respects even more that of Anthoceros. In the more primitive types, e.g., Marattiaceae, the large fleshy thallus might readily be mistaken for an Aneura, or Anthoceros, sometimes living for a long time and capable of multiplying by the detachment of branches. In Osmunda, another primitive genus, the gametophyte has a thickened midrib and unistratose wings like that of several anacrogynous liverworts, e.g., Mörkia and Calycularia. Gleichenia, another primitive fern, has a very similar gametophyte. Another type is found in some of the filmy ferns-Hymenophyllaceae, and species of Schizaea. These sometimes have filamentous gametophytes suggesting the protonema of a moss. Since such filamentous gametophytes can be induced in the common ferns by germinating the spores in water, it seems probable that this condition is secondary and due to the conditions under which the plants are grown.

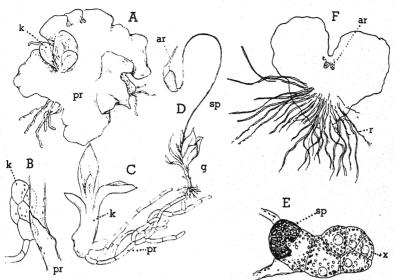


Fig. 15.—A, thallose protonema of Sphagnum; k, young leafy shoot; B, C, filamentous protonema of a moss, Funaria, with young leafy shoots; D, leafy shoot of Funaria, bearing the sporophyte, sp; E, young gametophyte (prothallium) of a fern, Onoclea; sp, spore membrane; F, older prothallium, with young archegonia, ar.

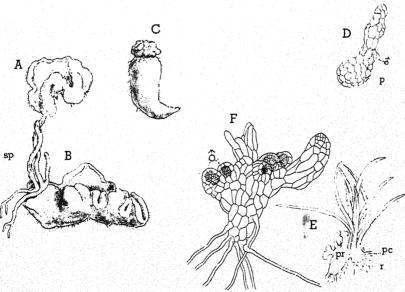


Fig. 16.—Gametophytes of Lycopodium and Equisetum. A, Lycopodium clavatum; B, L. annotinum; sp. young sporophytes; C, L. complanatum; D, young prothallium of L. cernuum; E, older prothallium; pr, bearing the young sporophyte; F, young male prothallium of Equisetum maximum; S, antheridium.

EOUISETINEAE

The horse-tails, Equisetineae, have only a single living genus, Equisetum. The gametophyte, which may attain considerable size, has much in common with the lower ferns but differs in some details. The sex organs, and especially the large spermatozoids, are very similar to those of the lower ferns.

LYCOPODINEAE

The Lycopodineae, like the Equisetineae, are much less numerous than the ferns. The more primitive forms are the "club mosses," of the genus Lycopodium, which show marked differences in the gametophytes in some of the species, indicating that the genus should be separated into several. The simplest type of gametophyte is seen in L. cernuum. It is a small cylindrical body, the base embedded in the ground, the top surrounded by a series of green lobes. In most of them the gametophyte is a subterranean tuberous structure quite destitute of chlorophyll. Similar subter-

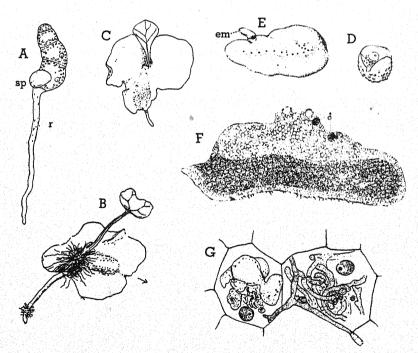


Fig. 17.—Gametophytes of Filicineae. A, germinating spore of a fern, Onoclea; B, prothallium of Osmunda Claytoniana, with attached sporophyte; C, Danaea jamaicensis; D-G, Botrychyum virginianum; D, germinating spore; E, gametophyte, with embryo-sporophyte, em; F, section of prothallium, the shaded portion occupied by the endophytic fungus (mycorrhiza); G, cells containing the mycorrhiza.

ranean gametophytes occur in one order of ferns—the Ophioglossales, and in the Psilotales.

As these subterranean gametophytes, having no chlorophyll, are incapable of photosynthesis, they are obliged to depend upon an association with a fungus (mycorrhiza) which lives within the tissues of the gametophyte and through which they apparently obtain their organic food. This "symbiosis" is presumably beneficial to both members of the association.

The constant association of a blue-green alga, Nostoc, with the Anthocerotaceae is perhaps also a somewhat similar case of symbiosis.

THE ARCHEGONIUM

The structure of the archegonium is essentially the same in all the lower embryophytes (Archegoniatae). A true archegonium, although greatly reduced in structure, occurs also in the simpler seed plants.

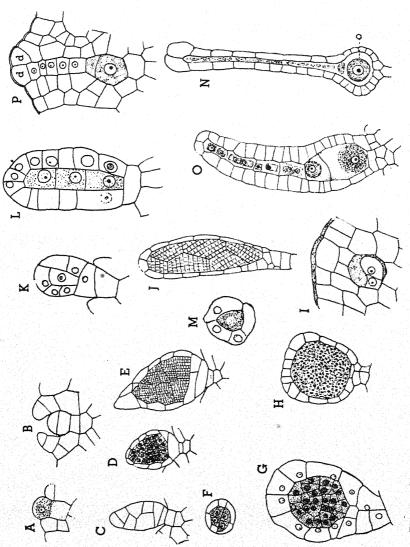
The flask-shaped archegonium of the Hepaticae arises from a superficial cell which usually first divides transversely into a basal or stalk cell, and a terminal cell which forms the body of the archegonium. The archegonium mother cell by the formation of three vertical intersecting walls is divided into an axial cell and three peripheral ones—from the latter are formed the five or six series of neck cells; from the axial cell by a transverse division a cap cell is cut off; and from the inner cell by successive transverse walls is developed an axial series of cells of which the lowermost is the egg cell and the others are the canal cells. The cap cell most commonly is divided into four by intersecting walls; but there is a good deal of variation in the number of cover cells. In the mosses the cap cell may divide repeatedly and contribute to the elongation of the neck.

In the Anthocerotes the mother cell of the archegonium does not project above the adjacent superficial cells, and the basal or ventral region is entirely coherent with the surrounding tissues. The neck is much shorter than that of the other bryophytes. In the Anthocerotes—and this has also been noted in some of the primitive ferns—the primary axial cell is cut out by three intersecting walls, much as in the Hepaticae, and the formation of egg, canal, and cover cells is much the same.

In the ferns the axial cell (usually considered to be the mother cell of the archegonium) divides into a conspicuous cover cell and an inner one. The cover cell divides by cross walls into four, and these by a series of transverse divisions give rise to the neck, which thus has four rows of cells instead of the five to six of the Hepaticae, and is homologous not with the whole neck of the latter but only with the cover cells. The primary canal cell is cut off subsequently from the inner cell and elongates with the growth of the neck cells. The canal cell usually divides but

once, and the division generally is confined to the nucleus. From the central cell, a second canal cell—the ventral canal cell—is later separated.

The archegonium of some species of Lycopodium is much more like that of the typical bryophytes. The neck is elongated and in cross section shows five to six cells, recalling the archegonium of the mosses. There may be also a large number of canal cells—as many as sixteen having been recorded—and some of these were binucleate. Details of the development of the archegonium, however, are incomplete. With the development of



development of antheridium in Riccia; G-H, antheridia of Calycularia; a moss, Funaria; antheridium of of bryophytes. Dendroceros; Fic. 18.--Gametangia young antheridium of

heterospory the archegonium becomes somewhat reduced, the neck is shorter, and the neck canal cell may remain undivided.

Among the lower seed plants (gymnosperms) there is a still greater reduction. The neck canal cell may be entirely suppressed and the ventral canal cell represented by a free nucleus, which is often evanescent and easily overlooked. Finally in the flowering plants (angiosperms) no definite archegonium is developed, and the egg cell is free in the cavity of the embryo sac.

THE ANTHERIDIUM

The antheridium of the Hepaticae shows a somewhat greater range of structure than the archegonium. The simplest type is found in *Sphaero-carpus*. It arises as a papillate superficial cell which is cut off by a transverse wall and then divides into a stalk cell and the body of the young antheridium, which is nearly globular.

In the Jungermanniales the first division wall is vertical and divides the cell into equal parts. In each of these halves two other vertical walls intersect each other and also the median wall. A cross section of the young antheridium shows two central triangular cells and four peripheral ones. There is usually a conspicuous stalk, which may be much elongated.

In the typical mosses the young antheridium grows for a long time from an apical cell, and the older antheridium is an elongated or clubshaped organ with a short, thick pedicel.

The inner tissue in all the bryophytes divides repeatedly and the small spermatocytes are very numerous. These are also known as "androcytes." After the final division in the spermatogenic tissue, the resulting pair of androcytes may remain together. This is usually the case in the Hepaticae, but it is not so evident in the mosses.

Before the final division two blepharoplasts may be seen, which occupy the poles of the nuclear spindle. There is some uncertainty as to the nature of these bodies—whether they are permanent organs of the cells, perhaps equivalent to centrosomes, or whether they arise de novo in the later phases of the spermatogenic tissue.

The nucleus of the androcyte is conspicuous and the blepharoplast lies near the periphery of the photoplast. The blepharoplast elongates, and is sometimes broken up into separate granules which gradually fuse; and it finally becomes a slender curved rod from which two long cilia develop. In the meantime the nucleus gradually forms a slender curved filament, staining strongly with usual nuclear stains. The blepharoplast is closely appressed to the elongated nucleus which forms the major part of the spermatozoid. A part of the cytoplasm of the spermatocyte remains attached to the spermatozoid.

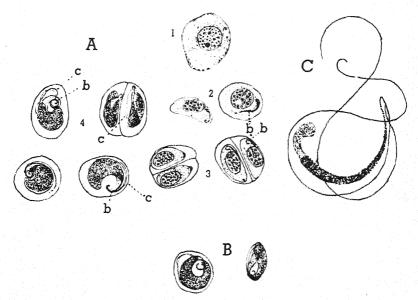


Fig. 19.—A, B, spermatogenesis in Calycularia radiculosa; b, blepharoplast; c, cilia; C, free spermatozoid of Pellia.

Anthocerotes.—In the Anthocerotes the antheridia, instead of originating from superficial cells, are formed from the inner of two cells resulting from the transverse division of a surface cell. Thus the antheridium lies within a closed cavity. The mother cell may form a single antheridium, or it may divide longitudinally into two or more cells, each of which develops into an antheridium. The antheridium resembles in form that of the Hepaticae. The spermatozoids are small and are not noticeably different from those of the typical liverworts.

Pteridophytes.—The antheridium of the pteridophytes is less specialized than that of the Hepaticae and mosses, and especially in its younger stages it recalls that of the Anthocerotes. In some of the more primitive ferns, like the Marattiaceae and the Ophioglossaceae, it might even be compared to the "gametangia" of some algae. The mother cell divides by a transverse wall into a cover cell and an inner one exactly as in Anthoceros; but instead of the inner cell forming a definite antheridium it develops into a mass of spermatocytes, each containing a large multiciliate spermatozoid. The cover cell divides several times. Often one of these cells forms an operculum which marks the opening through which the spermatozoids are discharged.

The antheridium of the Equisetineae, Psilotineae, and Lycopodium is much like that of the lower ferns (Eusporangiatae); but in the more

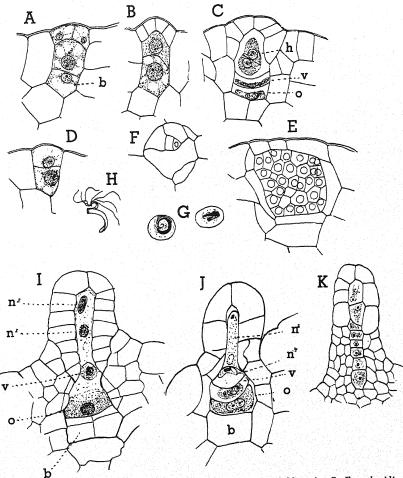


Fig. 20.—Gametangia of pteridophytes. A, B, C, archegonia of Marattia; D, E, antheridia of Marattia; F, surface view of antheridium; o, opercular cell; G, H, spermatozoids; I, archegonium of Botrychium; J, Equisetum; K, Lycopodium.

specialized ferns (Leptosporangiatae) the mother cell of the antheridium projects above the surface of the gametophyte forming a dome-shaped body with a single layer of parietal cells and a central cell from which the spermatocytes are derived.

Of the four classes of the pteridophytes the Lycopodineae show the nearest approach to the bryophytes in the structure of the archegonium, and they are the only pteridophytes in which the spermatozoids are biciliate like those of the bryophytes. It is not impossible that these similarities may indicate a real relationship. The other three classes, viz., Fili-

cineae, Equisetineae, and Psilotineae, differ from the Lycopodineae in having large multiciliate spermatozoids and constitute the "Polyciliatae."

In some of the heterosporous ferns, e.g., Marsilea, the gametophyte may be retained within the microspore until the spermatozoids are ready to be discharged. In Isoetes, the most reduced of all the pteridophytes, there is only one vegetative cell and only four spermatozoids are produced.

The transition from the heterosporous pteridophytes to the spermatophytes, so far as the male gametophyte is concerned, is a very gradual one. The most marked feature in the spermatophytes is the development of the pollen tube from the germinating microspore. In two of the most primitive of the existing spermatophytes, the monotypic Ginkgo and the cycads, the male gametes are large multiciliate motile spermatozoids, recalling those of the eusporangiate ferns. In Ginkgo there are two spermatozoids, and this is the case in most of the cycads.

In the conifers the pollen spores when shed may show no vegetative (prothallial) cells—e.g., Cupressus, Sequoia—or there may be a varying number—e.g., two in Pinus, and several in Araucaria and Podocarpus. In all of the conifers there is a primary generative cell which divides into a "stalk cell" and a body cell, the latter forming the two nonmotile male gametes. There are therefore in the germinating pollen spores four nuclei, the stalk nucleus, the two gametes, and the nucleus of the pollen tube.

The germination of the pollen spore of the angiosperms is very much like that of many conifers. As a rule no prothallial cell is present and the first nuclear division forms a generative and a tube nucleus, the former not infrequently being enclosed in a definite cell. No stalk cell is present, and the generative cell (or nucleus) divides at once into the two male gametes.

HOMOLOGIES OF THE SEX ORGANS (GAMETANGIA)

While the Ulothricales seem to be the nearest algal relatives of the embryophytes, their very simple reproductive organs—generally single cells—are very different from the characteristic archegonia and antheridia of the archegoniates.

There is a certain similarity in the sex organs of the Charales and those of the archegoniates, but it is hardly likely that the latter have been derived from such extremely specialized organisms as the Charales.

There have been various attempts to homologize the reproductive organs of the archegoniates with the "plurilocular" gametangia of the algae. Davis¹ has compared the free elongated gametangia of such brown algae (Phaeophyceae) as *Cutleria* and *Ectocarpus* with the archegonium of the typical Hepaticae. From such gametangia in which all the cells are

¹ B. M. Davis, "The Origin of the Archegonium," Ann. Bot., 17: 1903.

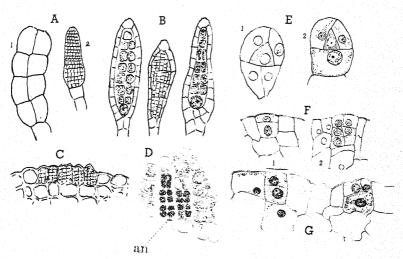


Fig. 21.—Evolution of the gametangia of the archegoniates. A, 1, female gametangium of the alga, Cutleria; A, 2, gametangium of Ectocarpus (after Smith); B, hypothetical intermediate forms between algae and archegoniates; C, plurilocular gametangia of Punctaria (A, B, after Davis; C, after Kjellmann); D, antheridia of Coleochaete scutata; E, 1, antheridium; E, 2, archegonium of Calobryum; F, young antheridia of Ophioglossum pendulum; G, young archegonia of Danaea elliptica.

fertile, by the sterilization of the outer layer of cells a structure comparable to an archegonium might result. Davis, however, recognizes that it is very improbable that there is any real relationship between these marine brown algae and the pure green archegoniates. He suggests that gametangia resembling those of *Ectocarpus* may also have developed among the Chlorophyceae, and cites *Schizomeris* and *Draparnaldia* as showing a tendency to development of such gametangia.

Miss Lyon¹ has compared the sunken gametangia of certain brown algae, e.g., *Phyllitis*, *Punctaria*, with the antheridia of the lower pteridophytes. She also refers to the gametangia of *Ulva*. Attention is also called to a number of interesting cases showing evidence of the basic likeness in the structure of the archegonium and antheridium in the archegoniates.

In Coleochaete, one of the Ulothricales, which in some respects resembles the hypothetical primitive archegoniates, the antheridial cells may, e.g., C. scutata, be grouped in what might be called a plurilocular gametangium. There is evidence that the archegonium, as well as the antheridium, in the archegoniates has been derived from some type of plurilocular gametangium, and that the two are homologous. This is especially evident in the development of these organs in the lower pteridophytes, notably the eusporangiate ferns—where the earliest stages are practically

¹ F. M. Lyon, "The Evolution of the Sex Organs of Plants," Bot. Gaz., 37: 1904.

identical. Even in the highly specialized mosses and leptosporangiate ferns, structures intermedial in character between archegonia and antheridia sometimes occur. Structures producing both eggs and spermatozoids have been repeatedly described. In the liverwort *Calobryum Blumei* the young archegonium and antheridium are practically indistinguishable and there is some evidence that the mature organ may possibly develop both sorts of gametes.

The nearest approach to the plurilocular gametangium of the algae, occurring in the embryophytes, is found among the more primitive pteridophytes. In these the mother cell of the antheridium divides into a superficial cover cell and an inner cell, the latter producing a mass of spermatids which might very well be called a plurilocular gametangium. In this respect the lower pteridophytes are more primitive than any of the bryophytes.

Whether the free antheridium and archegonium of the mosses and Hepaticae have been derived from a submersed type, or vice versa, or whether each type has originated independently, it is quite impossible to decide.

It is highly probable that the ancestors of the polyciliate pteridophytes had also polyciliate spermatozoids and were not derived from the same stock as the biciliate bryophytes and Lycopodineae.

It is possible that polyciliate algae, like *Oedogonium*, may have arisen from remote biciliate ancestors; but it seems unlikely that the large multiciliate spermatozoids of the ferns and *Equisetum* have originated independently from the small biciliate spermatozoids of the bryophytes, rather than from ancestors in which the multiciliate sperms inherited from similar algal types had already been developed.

CHAPTER IV

THE SPOROPHYTE

Assuming that the embryophytes have been derived from some algal ancestors and that the sporophyte is an elaboration of the unicellular zygote, or resting spore resulting from the union of the gametes, we may say that the sporophyte of the embryophytes, like the zygote of the alga, represents the terrestrial phase of the organism compared with the aquatic or amphibious gametophyte. As the terrestrial habit becomes more pronounced, the sporophyte assumes increasing importance until finally it becomes the dominant phase in the life cycle.

While there is a wide gap between the zygote of any known alga and the simplest known sporophyte in the liverworts, nevertheless a comparison of the two is instructive and may help to explain the origin of the sporophyte in the lower archegoniates.

The marked increase in size of the zygote of Coleochaete after fertilization and the development from it of a globular cell mass on germination are hints of what may have been the first step in the formation of a true sporophyte and strongly suggest what actually occurs in the early development of the sporophyte in Riccia, at present the simplest known among the archegoniates.

Since the zygote in both cases is diploid, it follows that a reduction division must occur before the spores are formed; and in *Coleochaete* this takes place at the first nuclear division in the zygote, and all the subsequent cells and the zoöspores developed from them are haploid. In the archegoniates the reduction division, so far as is known, does not take place until the first division of the spore mother cells which, like all the cells of the sporophyte, are diploid. However, the final results are the same and the spores, whether motile zoöspores of *Coleochaete*, or the nonmotile spores of *Riccia*, are haploid, and on germination produce haploid gametophytes.

In *Riccia* the fertilized ovum by repeated division and growth forms a globular multicellular "embryo," all of whose cells, except a single superficial layer, become spore mother cells. It may be assumed that in the first embryophytes all of the cells were sporogenous.

The further evolution of the sporophyte is associated with an increasing subordination of the sporogenous or "fertile" tissue to "sterile" vegetative tissue. This "sterilization" of potentially sporogenous cells, as the

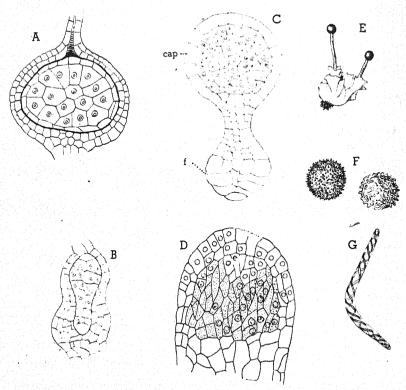


Fig. 22.—Sporophyte of Hepaticae. A, young sporophyte of Riccia, the nucleated cells are sporogenous; B, C, Sphaerocarpus; cap., capsule wall; f, foot; D, young capsule of Podomitrium; the sporogenous tissue (archesporium) shaded; E, Fossombronia longiseta, with two sporophytes; F, ripe spores; G, elater of Fossombronia.

most potent factor in the evolution of the sporophyte, has been treated at length by Professor F. O. Bower. The theory of progressive sterilization explains the increasing importance of the sporophyte in the history of the land plants. Whether the simple sporophyte of *Riccia* is really primitive or is reduced from some more specialized type, at any rate it illustrates what may have been the first steps in the evolution of the sporophyte.

The next stage may be illustrated by some of the lower Hepaticae, e.g., Sphaerocarpus. In the latter, the first division (basal wall) in the embryo is transverse and separates a lower (hypobasal) sterile region from the upper (epibasal) sporogenous portion. The former develops into a globular haustorium or "foot," through which the embryo receives nourishment from the parent gametophyte upon which the young sporophyte is therefore parasitic. In the epibasal region there is, as in Riccia, a peripheral layer of sterile cells, and a central mass of sporogenous tissue. While in

Riccia all of the latter cells become functional spore mother cells, in Sphaerocarpus some of them remain undivided and probably function as nutritive cells for the developing spores. In most of the Hepaticae these sterile cells become greatly elongated and develop spiral thickenings on the cell walls. These "elaters" when mature are highly hygroscopic and presumably are mainly concerned with the dehiscence of the ripe spore capsule and the scattering of the spores. In many of the Hepaticae there is developed between the foot and the spore capsule a stalk, or seta, which at maturity rapidly elongates and thus assists in the distribution of the spores.

The growing embryo remains for a long time enclosed in the venter of the archegonium, which keeps pace with the developing sporophyte. The envelope formed from the archegonium-venter is the "calyptra."

HEPATICAE

The Hepaticae form a natural class and agree pretty closely in the essential characters of the sporophyte. Aside from the Ricciaceae the least-specialized sporophyte is found in the Sphaerocarpales, which, on the whole, are the most primitive of the Hepaticae and to some extent may be considered as intermediate in character between the other two orders usually recognized, the Marchantiales and Jungermanniales, which might be regarded as divergent lines derived from ancestral forms related to Sphaerocarpus.

A very large majority of the Hepaticae belong to the Jungermanniales. The development of the sporophyte is completely known only in relatively few species; but for the most part the embryology is sufficiently alike to indicate that, like the Marchantiales, the Jungermanniales constitute a really natural order.

In the Hepaticae the growth of the sporophyte is probably limited by the small amount of green tissue. Chlorophyll is present in the young capsule but is limited in amount, and the developing sporophyte is very largely dependent upon the gametophyte for its food supply. The whole development of the sporophyte is immediately concerned with the production and dispersal of the spores. After the spores are shed there is a complete collapse of the rest of the sporogonium.

In the two other classes of the bryophytes, the mosses (Musci) and "horned liverworts" (Anthocerotes), there is a marked reduction in the sporogenous tissue and a decided increase in the amount and the degree of specialization of the sterile or vegetative structures. Consequently the growing period of the sporophyte is much prolonged, owing especially to the development of chlorophyllous tissues which permits photosynthesis and therefore enables it to manufacture part, at least, of its necessary

food; and except for its water supply it is largely independent of the gametophyte. The least specialized of these are the Anthocerotes.

The Anthocerotes form a very natural group, and so evidently are all related that they may be readily referred to a single family, Anthocerotaceae. Their relation to the Hepaticae is somewhat doubtful. Although the gametophyte is less differentiated than in most Hepaticae, the sporophyte, even in the least-specialized forms, is a decided advance upon that of the Hepaticae.

In the genus Anthoceros the conditions approach those of the simplest vascular plants. At an early period there is formed between the foot and the sporogenous region of the embryo a zone of rapidly growing tissue

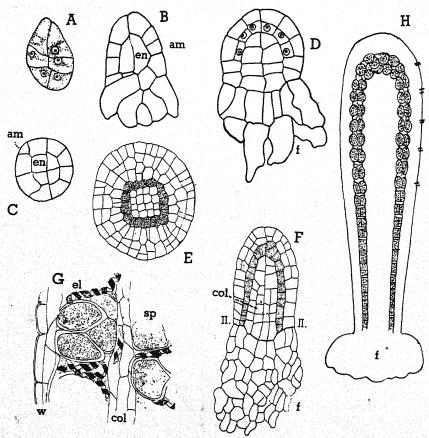


Fig. 23.—Development of the sporophyte in Anthocerotes. A, B, young embryos of Anthoceros; C, cross section of young embryo; D, E, older stages, showing origin of the archesporium; F, an older embryo of Dendroceros; G, section of older sporophyte of Dendroceros, showing spore tetrads, and elater-like sterile cells; H, diagram, showing development of fertile and sterile areas in the archesporium.

(meristem) which may retain its activity for several months. The sporogenous tissue (archesporium) is restricted to a single layer of cells enclosing an axial cylinder "columella," which sometimes, at least, seems to be an efficient conductor of water absorbed by the large foot which is in close contact with the tissues of the gametophyte.

Outside the archesporium is an envelope of several layers of chlorophyllous cells, the outermost forming an epidermis provided with stomata like those in the leaves of vascular plants. There is thus an efficient photosynthetic apparatus. Water, however, is absorbed from the gametophyte through the foot. Were the latter in direct contact with the soil, so as to obtain water directly, the sporophyte might then sever its connection with the gametophyte and become an independent plant. This is what actually happens in the lower ferns, where a root is developed which penetrates the gametophyte and fastens the young sporophyte to the substratum, thus starting it on its career as a long-lived leafy plant.

In Anthoceros, following the octant divisions, a second transverse division occurs and the embryo consists of three tiers each consisting of four equal cells. The two lower tiers develop into the large foot. The upper tier, by further transverse divisions, is separated into a terminal segment, in which the archesporium arises, and an intermediate zone between this and the foot. A series of periclinal divisions establishes the axial "endothecium" and the "amphithecium." At this stage the embryo has some resemblance to a corresponding stage in Fossombronia, a liverwort belonging to the Jungermanniales. There is also a marked similarity to the embryo of Sphagnum, the most primitive of the mosses. In both Sphagnum and Anthoceros the sporogenous tissue arises from the amphithecium, and the form of the two embryos is very similar. Comparing the embryo of Fossombronia and Anthoceros the terminal segment in Anthoceros might be likened to the capsule in Fossombronia and the intermediate segment to the seta.

In the intermediate segment in Anthoceros rapid cell division goes on and the apical region of the young sporophyte is thus pushed up and rapid elongation results so that ultimately the sporophyte may attain a length of ten centimeters or more. When ripe the elongated sporophyte splits at the apex into two valves, which open gradually with the progressive ripening of the spores in the younger portions. The sporophyte of the Anthocerotes has suggestions of both the Hepaticae and the Musci, but it is questionable if these resemblances are really homologies and indicate a genetic relationship.

Still more interesting is the approach to complete independence shown by *Anthoceros* foreshadowing the conditions actually found in the simplest vascular plants.

THE SPOROPHYTE-PTERIDOPHYTES

In the Musci the reduction of the sporogenous tissue is much greater than in the Hepaticae, and the sporophyte may have a long period of growth associated with a very perfect photosynthetic apparatus. Well-developed conducting tissues and an elaborate mechanism for the dispersal of spores are also found. All of these structures, however, are concerned primarily with spore distribution, and only in a very few cases is there any tendency for the sporophyte to sever its connection with the gametophyte. As soon as the spores are shed, the sporophyte collapses completely. The elaboration of the sporophyte in the mosses is to a great extent paralleled by that of the gametophyte, the most specialized sporophytes, e.g., *Polytrichum*, *Dawsonia*, being associated with the most highly developed gametophytes.

Unlike the Hepaticae the gametophyte in the Musci has become adapted to extremely varied conditions and thus can compete, to some extent, with the vascular plants. This may, perhaps, explain the relative unimportance of the sporophyte and the fact that it is rarely developed in many species which depend almost entirely on the vegetative propagation of the gametophyte.

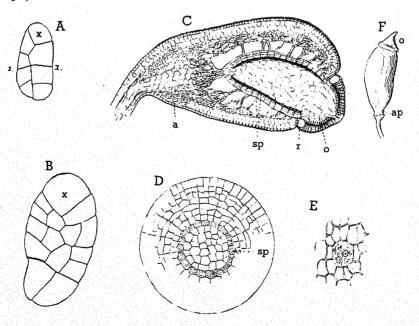


Fig. 24.—Musci. A, B, embryos of Funaria showing the apical cell, x; C, section of nearly mature capsule; a, apophysis; sp, sporogenous tissue; r, annulus; o, operculum; D, cross section of young sporophyte; sp, archesporium; E, young stoma, from the apophysis; F, capsule of Polytrichum; ap, apophysis; o, operculum.

In the Anthocerotes, however, conditions are very different. The simple gametophyte is dependent upon an ample water supply, while the sporophyte is relatively large and, as in the Musci, develops abundant chlorophyll and may continue its growth for a long time. Unlike the mosses, these develop no elaborate mechanism for spore distribution, and the sporophyte remains a simple cylindrical body which develops new sporogenous tissue from its basal meristem and continues its growth long after the first spores are shed—in short, the dispersal of the spores does not end the life of the sporophyte as it does in both Hepaticae and Musci.

Through the massive foot, which encroaches more and more on the surrounding gametophytic tissue, the sporophyte obtains the water needed for its growth; and there is a possibility that it may in some cases destroy the ventral tissue of the gametophyte and come into direct contact with the substratum, thus emancipating itself completely from the gametophyte. In *Anthoceros*, therefore, a condition exists closely approaching what we may believe preceded the appearance of the true "vascular" plants.

Our knowledge of the fossil bryophytes is so scanty and fragmentary that we are perforce almost entirely dependent upon a comparative study of living forms for data bearing on this phylogeny. Compared with the bryophytes the "vascular" plants have left abundant and sometimes very perfectly preserved fossil remains which throw much light upon their early history. Of special interest in this connection are the important discoveries made by British and German investigators, during the past two decades, of certain fossils in the older Devonian rocks.

In the higher mosses the stalk (seta) of the sporogonium has a central strand of elongated cells which is, with little question, concerned with the transport of water. In the Anthocerotes there is a similar axial structure, the "columella," which may be compared with the conducting strand of the mosses; but in most cases it may be questioned how far it functions

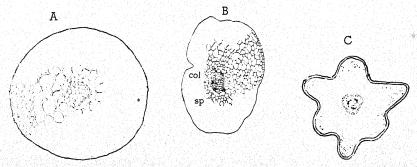


Fig. 25.—A, cross section of seta of Funaria; B, section of a large sporophyte of Anthoceros fusiformis, showing conspicuous central strand, col; C, section of stem in Tmesipteris, with central vascular cylinder.

as a conducting system. It may, however, under special conditions, become greatly enlarged and probably acts as a definite conducting apparatus. This conducting tissue becomes highly developed in all of the higher embryophytes and forms a definite "fibro-vascular" system of tissues, and all of the forms above the bryophytes are generally known as "vascular plants."

The most characteristic element of the fibro-vascular bundle is the "tracheary" tissue, composed of either single elongated cells—tracheids—or of tubes made up of a series of cells—vessels. The tracheary elements, when mature, are destitute of protoplasmic content and have the cell walls thickened and lignified. There are commonly characteristic sculpturings of the thick-end walls. These woody, water-conducting elements, with a greater or less amount of parenchyma, constitute the "xylem." Outside of the xylem—sometimes completely surrounding it—is the "phloem" whose elongated elements usually have cellulose walls. Some of the larger elements are "sieve tubes."

The simplest vascular bundle, e.g., in *Rhynia*, is a cylinder of elongated cells with a few axial tracheids surrounded by undifferentiated cells, considered to represent phloem. This has been called a "protostele," and from this assumed primitive type it is believed by many investigators that all of the complicated fibro-vascular structures in the axes of the higher vascular plants have been evolved; and in most cases constitute a single unit or "stele."

As the woody tissues are very resistant and are often very perfectly preserved, they are extremely important in a study of fossil plants; but it may perhaps be questioned whether the stress laid on the importance of these skeletal structures in classification has not been somewhat over-emphasized in comparison with other structural features.

It is certain that in some of the more primitive ferns, e.g., Ophioglossum and Marattiaceae, the complicated vascular skeleton of the axis is not a single stele but is made up of the junction of many independent strands (leaf traces); and it is possible that a similar condition occurs in many other ferns.

The arrangement of xylem and phloem, as well as the form of the elements of the two regions, of course varies greatly and is of much importance in a comparative study of the main phyla of the vascular plants.

The most obvious distinction between bryophytes and pteridophytes, the most primitive vascular plants, is the development of the sporophyte of the latter as an independent plant; but this independence, as already indicated, was doubtless a rather gradual process. Thus there are still pteridophytes in which the gametophyte persists for a long time and may propagate itself vegetatively. Such gametophytes, e.g., species of Equisetum, Lycopodium, and Danaea, may also produce several sporophytes

which remain for a long time attached to the gametophyte. Sooner or later, however, the sporophyte becomes entirely independent and typically develops definite external organs—stem, leaf, and root. Ultimately the sporophyte in some of the pteridophytes may assume tree-like dimensions, as in the living tree ferns and the fossil Calamites and Lepidodendron. In such cases the production of spores is postponed for many years and is restricted to definite organs—"sporangia." Sporangia are recognizable as such in the earliest vascular plants before definite stem and leaves are present; and the sporangium must be recognized as an organ, sui generis, and not as a modification or metamorphosis of stem or leaf structures. The evolution of the sporangium, as shown by both the fossil

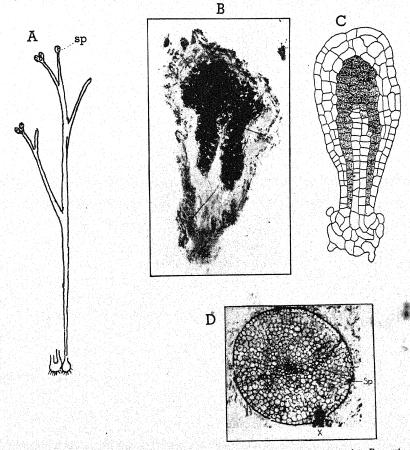


Fig. 26.—A, Hornea, one of the earliest known vascular plants; sp, sporangia; B, section of sporangium; C, young sporophyte of Notothylas, one of the Anthocerotales, showing a similar arrangement of the sporogenous tissue; D, section of Rhynia (A, B, D, after Zimmermann).

record and the comparative anatomy of the more primitive living types, and its structure, is perhaps the most important factor in the classification

of the pteridophytes.

The simplest known vascular plants are two genera, Rhynia and Hornea, first described by Kidston and Lang¹ from the Lower Devonian of Scotland. These were slender leafless plants, sometimes hardly exceeding in size the sporophytes of some species of Anthoceros. They were occasionally unbranched but commonly dichotomously divided into a few branches. In Rhynia the upright shoots arose from a prostrate rhizome, but there were no true roots. In Hornea the sporogenous tissue formed a thick dome-shaped mass enclosing a "columella" like that of Sphagnum, one of the primitive mosses, but still more like that of Notothylas of the Anthocerotaceae.

The shoot had a very simple vascular bundle composed of a central strand of tracheary tissue surrounded by undifferentiated parenchyma. A cross section of such a shoot, except for the few tracheids, is almost identical in appearance with a similar section of certain large sporophytes of *Anthoceros* in which the sporogenous tissue was almost completely suppressed and the columella greatly increased in size and apparently served as a very simple conducting organ (vascular bundle?).

Considering the extraordinarily close resemblance between the structure of these ancient pteridophytes and the sporophyte of the Anthocerotaceae, it is a fair assumption that the Rhyniaceae were derived either directly from some Anthocerotaceae or from forms very much like them.

The undifferentiated, cylindrical, dichotomously branched plant body of the Rhyniaceae has been named a "telome" by Zimmermann.² The same term has been applied also to similar structures in some other primitive forms.

Of the existing pteridophytes, one small family, Psilotaceae, has a good deal in common with the Rhyniaceae; and the two families may be placed in a common class. Psilotineae.

Besides the Rhyniaceae there are also found in the older Devonian rocks some more highly organized types, which it has been claimed may be regarded as prototypes of the other three classes of pteridophytes, viz., Lycopodineae (club mosses), Equisetineae (horse-tails), and Filicineae (ferns). Just what relationship, if any, existed between these and the Rhyniaceae is still a question.

In the club mosses and horse-tails it is the axis of the shoot which is of primary importance, and this axis or stem bears the simple leaves as

¹ R. Kidston and W. H. Lang, "Old Red Sandstone Plants from the Rhynie Chert," *Trans. Roy. Soc. Edinb.*, 1-5: 1917-1921.

² W. Zimmermann, Die Phylogenie der Pflanzen, Jena, 1930.

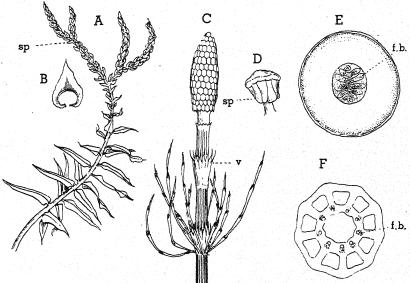


Fig. 27.—A, Lycopodium pachystachyon; sp, sporophylls; B, single sporophyll; C, Equisetum limosum; D, sporangiophore with pendent sporangia; E, cross section of stem in Lycopodium dendroideum; f.b., the vascular bundles; F, section of stem in Equisetum arvense.

appendages. In the lycopods the stem is usually quite solid with a central massive vascular bundle or "stele," much as in *Rhynia*. In the Equisetineae the stem is jointed and usually hollow with a circle of smaller independent vascular bundles.

Among the Devonian genera, Asteroxylon possibly is related to the Lycopodineae and Calamophyton and Hyenia to the Equisetineae (Articulatae).

In the fern series the development of the plant body has been very different. Among the Devonian fossils are types which show a dichotomously branched structure suggesting the thallus of certain algae or some Hepaticae. This flattened "telome" recalls the dichotomously divided leaves of certain living ferns and in most ferns the primary leaf is usually dichotomous.

If we may judge from the analogy of the early development of the sporophyte in the lower ferns, e.g., Ophioglossaceae, and Marattiaceae, the primeval ferns had no stem but consisted of a foot or perhaps a root and a single fertile frond. That is, from the first the leaf was the essential structure, the stem a secondary one.

This condition actually exists in Ophioglossum moluccanum, where the young sporophyte consists of a leaf and root only. The definitive shoot

arises secondarily as a bud from the primary root. Perhaps the earliest condition was leaf and foot, as it is probable that in *Ophioglossum*, as in the Marattiaceae, the root is a secondary endogenous structure.

As the successive leaves increase in size their persistent bases unite to form the stem (caudex). The stem apex contributes but little directly to growth of the caudex, which is derived from the independent leaf traces. A few small "cauline" bundles are found in most Marattiaceae, but are wanting in the Ophioglossaceae.

THE EMBRYO

The early divisions of the embryo in the pteridophytes as a rule closely resemble those of the Hepaticae and the Anthocerotes. The basal wall is usually transverse to the axis of the archegonium as in the Hepaticae; but in the more specialized ferns it is vertical, recalling the embryo of Anthoceros. The epibasal region gives rise to the axis and foliar structures, the hypobasal to the foot, and sometimes the primary root. The young embryo, therefore, may be described as bipolar. Sometimes the first division wall cuts off a "suspensor," recalling the basal appendage so often found in the Jungermanniales. The significance of the suspensor is not entirely clear.

The embryo may reach considerable size before the organs of the young sporophyte are recognizable, and in general we may assume that

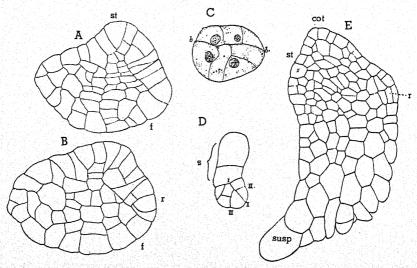


Fig. 28.—A, B, two sections of an embryo of Equisetum debile; st, stem apex; f, foot; r, possibly the root; C, a younger embryo; b, the basal walls; D, young embryo of Lycopodium phlegmaria; s, suspensor; E, an older embryo; susp, suspensor; st, stem apex; cot, cotyledon (D, E, after Treub).

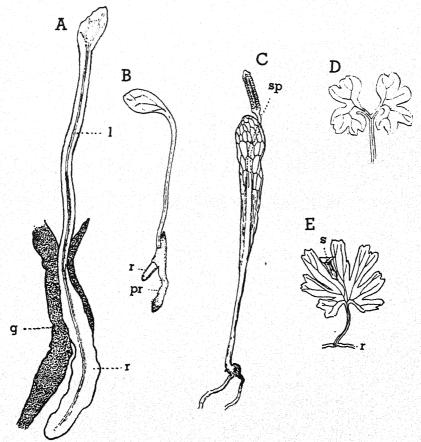


Fig. 29.—A, young sporophyte of Ophioglossum moluccanum consisting of cotyledon and root only; g, gametophyte; B, a similar case; C, O. intermedium; sp, sporangiophore; D, cotyledon of a typical fern, showing dichotomous venation; E, filmy fern, Trichomanes; s, sorus.

those forms in which early differentiation occurs are the more recent and specialized.

Bower¹ believes that the primitive type of embryo is an elongated bipolar body, the "primitive spindle," which develops into a primary shoot, or axis, bearing leaves and roots as appendages. While this theory is in harmony with the early development of the sporophyte in the microphyllous forms, it is difficult to reconcile it with the conditions in most of the ferns. While the young embryo of these may be regarded as bipolar, the leaf soon assumes the leading role in the development of the sporophyte and the stem may be completely suppressed in the young sporophyte of such

¹ F. O. Bower, Origin of a Land Flora, London, 1908.

exceptional cases as some species of Ophioglossum, a genus which for various reasons may be regarded as the most primitive of existing ferns.

The Psilotaceae are probably the nearest living relatives of the Rhyniaceae. The embryo of *Tmesipteris* closely resembles the condition found in *Rhynia*. The young embryo consists of a foot and a cylindrical shoot, which may branch dichotomously. No roots are developed. This shoot develops into a branching subterranean rhizome, from which later the green leaf shoots are developed.

In the Equisetineae, e.g., Equisetum debile, the massive foot may occupy the whole hypobasal region of the embryo; while in the epibasal region there is formed a conical body whose apex is occupied by a very conspicuous apical cell. The whole epibasal region thus forms the shoot or stem, which elongates rapidly and soon shows the characteristic nodes, each surrounded by a circle of small leaves. Each leaf is traversed by a single vascular bundle. The bundles unite at the nodes.

While the adult sporophyte of Equisetum and the ferns show little

resemblance, the embryos show some marked similarities.

Most of the existing ferns are often placed in a single family, Polypodiaceae. In these the first divisions of the embryo divide it into equal quadrants, which become the initials for the primary organs—stem, leaf (cotyledon), root, and foot. In these ferns the root is of superficial origin, developing at once from one of the original quadrants of the embryo. Of the four quadrants the epibasal ones form the stem apex and the cotyledon, the hypobasal ones the root and foot; and except for the foot the apical cells of the different organs may be traced back to the original octant cells. The root and the cotyledon develop much more rapidly than in the more primitive ferns.

THE SPORANGIUM

It may be assumed that the ancestors of the pteridophytes were Anthoceros-like liverworts in which the sporophyte became entirely independent through the direct absorption of water from the substratum by the enlarged foot. The formation of a true root was probably a later development. With the appearance of tracheary tissue in the axial strand of conducting tissue, the transformation of the sporogonium into a "vascular" sporophyte would be complete. The fossil Rhyniaceae show a marked structural resemblance to this hypothetical ancestral form. Hornea is especially noteworthy, as the sporogenous region is comparable to that in some of the Anthocerotes, especially Notothylas. The bulbous "protocorns" of Hornea, like the foot of Anthoceros, is composed entirely of parenchyma. It is hardly likely, however, that the sporangia of all the existing pteridophytes can be traced back to the single terminal sporangium of the Rhyniaceae.

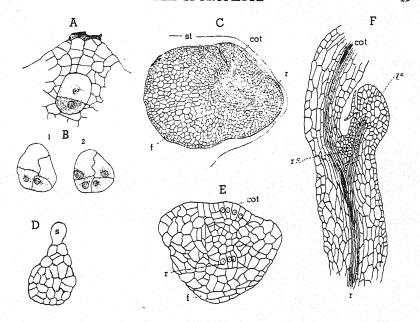


Fig. 30.—Eusporangiate ferns. A, two-celled embryo of Botrychium virginianum; B, two sections of a four-celled embryo of the same; C, older embryo, showing stem apex, cotyledon, root, and foot; D, young embryo of B. obliquum, showing suspensor, s; E, embryo of Danaea elliptica; cot, cotyledon; the root is endogenous; F, young sporophyte of the same, showing the union of the leaf bundles with the stele of the root; r², second root.

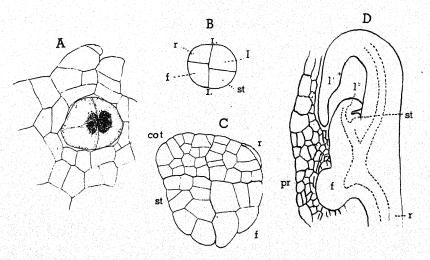


Fig. 31.—Leptosporangiate ferns. A, two-celled embryo of Onoclea; B, diagram showing the relations of the primary organs, stem, leaf, root, and foot; C, median section of an older embryo; D, section of young sporophyte, still attached to the gametophyte, pr.

The history of the sporangial structures shown by the fossil record, as well as the comparative anatomy of the more primitive living types, make it pretty clear that the sporangia are not primarily modifications of stem or leaf structures. While in the more specialized leptosporangiate ferns the sporangia arise from superficial cells of the leaf, in the primitive types, like *Rhynia* before the plant body was differentiated into stem and leaves, definite sporangia are present and the sporangium must be considered as a primary organ of the sporophyte and not a secondary one. In the more primitive types, the sporangia are often borne on special structures—sporangiophores. These are especially conspicuous among living forms in the Ophioglossaceae, and the Equisetaceae.

The structure of the sporangium in one of these less-specialized types may be illustrated by a fern, Botrychium, one of the Ophioglossaceae. In both Ophioglossum and Botrychium the fertile frond is composed of two parts, the sporangiophore and the sterile green lamina. The sporangiophore in Botrychium is pinnately divided into numerous branches, the final divisions bearing the globular sporangia. The young sporangium shows a central mass of sporogenous cells, which may be traced back to a single archesporial cell. Outside of the sporogenous tissue are several layers of parietal cells. The inner layers adjacent to the mass of sporogenous tissue, the "tapetum," are broken down and serve to nourish the developing spores. The young spore mother cells become rounded off and undergo the characteristic tetrad division, the resulting spores having the haploid chromosome number.

The character of the sporangium differs widely in the pteridophytes and is one of the most important factors in their classification. Of the existing pteridophytes, the small family Psilotaceae most nearly resembles the Rhyniaceae. The family includes only two genera, *Psilotum* and *Tmesipteris*. Like the Rhyniaceae these are rootless, and the dichotomously branched, practically leafless shoot of the former is suggestive of the structure of *Rhynia*.

The sporangia of the Psilotaceae are borne on short branches—or sporangiophores—and are partially united, forming a "synangium," with two spore masses in *Tmesipteris*, and three in *Psilotum*. There has been some controversy as to the origin of the synangium, but the more recent investigations indicate that the synangium arises from the apex of the sporangiophore and thus resembles the terminal sporangium of the Rhyniaceae.

FERNS (FILICINEAE)

The great majority of the existing pteridophytes are ferns, often of the family Polypodiaceae. In these the sporangium arises from the leaf sur-

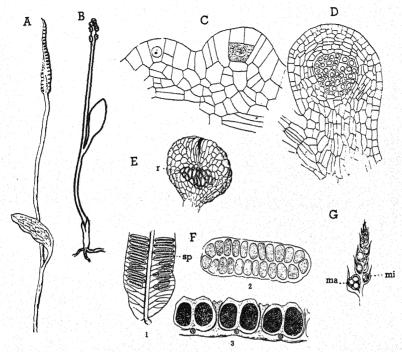


Fig. 32.—Sporangia. A, Ophioglossum, sporangia borne on an elongated sporangiophore; B, Botrychium simplex; C, young sporangia of B. virginianum; D, a later stage; E, ripe sporangium of Osmunda; r, the annulus; F, Danaea jamaicensis; F, I, lower side of the fertile leaflet with the elongated synangia; F, 2, horizontal section of a synangium; F, 3, a vertical section of three synangia; G, strobilus of Selaginella, showing megasporangia, ma; microsporangia, mi.

face as a single epidermal cell—in much the same way as a hair. These ferns are evidently a distinctly modern group, and with several other families, more or less evidently related, constitute the Leptosporangiatae.

Representing the more primitive ferns are two orders—Marattiales and Ophioglossales, in which the sporangia are much larger and less specialized than those of the Leptosporangiatae. These are the Eusporangiatae, which are relatively few in number and are mainly confined to the tropical and subtropical regions.

In the Ophioglossaceae the sporangia do not arise from the surface of the leaf but there is developed a special structure, the sporangiophore, which in some cases, at least—e.g., Ophioglossum moluccanum and Botrychium Lunaria—is formed by a dichotomy of the very young frond into a fertile and sterile portion, viz., sporangiophore and leaf. In Ophioglossum the sporangiophore is a flattened spike. The sporangia form a single row on each margin but are scarcely perceptible in the early stages. Each sporan-

gium consists of a large mass of sporogenous tissue deeply sunk below the surface. Bower states that in the very early stages there is a continuous band of potentially sporogenous tissue below the margin on either side of the spike. This band later becomes differentiated into alternate fertile and sterile areas, the former marking the position of the future sporangia and giving rise to the large spore masses which when ripe are discharged through a cleft in the overlying tissue. This segregation of sterile and fertile areas in a potential sporogenous region or "archesporium" is very much like the condition in many Anthocerotes. This led the writer to suggest that the sporangiophore of Ophioglossum might have been derived from some Anthoceros-like ancestor where instead of a single terminal sporangium being formed, as in the Rhyniaceae, a series of lateral spore masses was developed, each discharging from an independent orifice. Such a structure might be comparable with the sporangiophore of a small Ophioglossum. Of course this hypothesis is purely conjectural, but it may be worth consideration.

From Ophioglossum, by branching of the sporangiophore and segregation of the individual sporangia, the condition in Botrychium may readily have been derived; but the connection with other ferns is not so evident.

The second order of the Eusporangiatae, the Marattiales, differs from the Ophioglossales in having the sporangia borne upon the lower side of the leaves, as in the common ferns. The sporangia are in most cases united into a solid synangium, but sometimes they are distinct but crowded together.

In the Polypodiaceae the sporangium can be traced back to a single epidermal cell of the leaf, and the divisions are very regular. In the Leptosporangiatae the dehiscence of the sporangium is effected by a characteristic apparatus, the annulus. In the Polypodiaceae this consists of a band of cells with thickened cell walls. The annulus extends over the top of the sporangium to the place where the sporangium opens. The cells of the annulus are markedly hygroscopic and when dry contract so strongly that a transverse rent is torn in the wall and the annulus springs back, tearing away the upper part of the sporangium and throwing the spores for a considerable distance.

Bower, who has made a very complete study of the sporangium of the ferns, emphasizes the reduction of the spore output in the Polypodiaceae and other presumably recent families of the Leptosporangiatae, compared with the older and more primitive families and still more compared with the Eusporangiatae. Thus he shows¹ that the average number of spores from a sporangium of the Polypodiaceae was from 48 to 64; while in

Osmunda regalis it was from 256 to 512. In several species of Gleichenia, another ancient type, it was from 256 to 1,024. In Kaulfussia, one of the Marattiaceae, it was 7,850.

EQUISETINEAE

In Equisetum, the only modern representative of the Equisetineae, the sporangia are borne on characteristic sporangiophores, arranged in crowded circles about nodes of the shoot apex, forming the conspicuous strobilus or cone of the fertile shoots. The sporangiophore is a shield-shaped (peltate) body with a short pedicel. The pendent sac-shaped sporangia are placed about the margin of the sporangiophore.

The development of the sporangium is somewhat like that of the Eusporangiatae; but is also reminiscent, both in form and in the structure of the wall, of the anthers of the flowering plants, rather than the sporangia of the other pteridophytes. Like the parietal cells of the anther, there are spiral and annular thickenings.

LYCOPODINEAE

In the Lycopodineae the sporangia are borne singly, upon the upper surface of a leaf usually, near its base, but sometimes from the axis, close to the leaf base. The sporophylls may differ but little from the sterile leaves, e.g., as in *Lycopodium lucidulum* and *Selaginella rupestris*; but usually they are reduced in size, often with little chlorophyll, and are closely aggregated into a definite strobilus or "cone."

The young sporangium in *Lycopodium* forms a transverse ridge near the base of the sporophyll. Sections show a transverse row of archesporial cells and a parietal layer of cells. From the archesporial cells, by repeated division, the sporogenous cells develop.

Selaginella agrees closely with Lycopodium in the development of the sporangium up to the time of spore division, but in some of the sporangia all of the mother cells divide as in Lycopodium, while in others only one mother cell, as a rule, divides and the others degenerate, so that the sporangium contains but four spores, which greatly exceed in size the other spores. These are the megaspores (macrospores) and the sporangium is the megasporangium. The smaller spores, microspores, closely resemble the spores of Lycopodium. From the megaspores are formed female gametophytes, and from the megaspores male. Selaginella is, therefore, "heterosporous."

HETEROSPORY

In most forns the spores are all alike, i.e., they are "homosporous" and produce gametophytes bearing both archegonia and antheridia. Occasion-

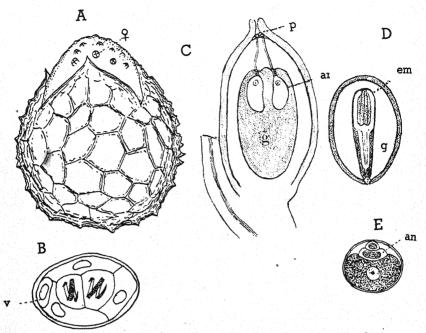


Fig. 33.—Heterospory and seeds. A, germinating megaspore of Selaginella, \mathcal{Q} , the female gametophyte; B, microspore of Isoetes, containing the greatly reduced male gametophyte; v, sterile prothallial cell, two of the four sperm cells are shown; C, megasporangium (ovule) of a pine; the embryo sac (megaspore) contains the large gametophyte with several archegonia, ar; p, pollen spores sending down the pollen tubes; D, ripe seed of the pine; g, gametophyte (endosperm); em, the young sporophyte; E, pollen spore (microspore) of Cycas; from the antheridial cells, an, two large ciliated spermatozoids are developed.

ally the gametophytes are unisexual, although the spores are all alike—e.g., Onoclea—and this is the rule in Equisetum. In such cases the males are smaller than the females. This segregation of the sexes is the first step in the direction of heterospory where there is a great reduction in sizes of the gametophytes, especially the males.

There are two families of heterosporous ferns, Marsileaceae and Salviniaceae, usually placed in a special order, Hydropterides; but they are evidently more nearly related to certain homosporous families than to each other. Another family, Isoetaceae, should probably also be associated with the ferns rather than with the Lycopodineae, as is more often done.

Like Selaginella, the sporangia in the Hydropterides, up to a certain point, are alike; but the subsequent development of the megasporangium differs very much from that of Selaginella. In Azolla, one of the Salviniaceae, the microsporangium and megasporangium are alike up to the last division in the archesporium. In the microsporangium there are sixteen spore mother cells; in the megasporangium only eight. In both cases the

tetrad division is completed; but in the megasporangium only one of the 32 spores matures, the others becoming disorganized and contributing to the growth of the single megaspore, which completely fills the cavity of the greatly enlarged sporangium. The ripe megaspore contains large amounts of starch and other foodstuffs, which permit the rapid development of the gametophyte and the young sporophyte developed from it. The growth of the gametophyte may be very rapid. In *Marsilea*, within less than twenty-four hours after the spores have been placed in water, the development of the gametophyte and fertilization may be completed.

While in the Hydropterides the spores are discharged before germination begins, in Selaginella the gametophyte begins to develop within the young megaspore while it is very small and contains but little cytoplasm, the growth of the gametophyte within the spore depending not on stored food material but upon material conveyed through the tapetal cells, which are in intimate contact with the spore membrane. The developing gametophyte is, therefore, in a sense parasitic upon the sporophyte, thus reversing the condition in other archegoniates where the young sporophyte is nourished by the tissues of the gametophyte. It is not until a later stage of the megaspore that food materials are "stored" which provide for the final stages of the gametophyte after the spores are shed as well as for the young sporophyte.

It is not a very long step from the condition found in *Selaginella* to the formation of seeds where the megaspore is retained permanently within the megasporangium, which usually remains attached to the sporophyte until after fertilization.

That heterospory has arisen independently in numerous unrelated phyla is amply demonstrated both by the fossil record and by a study of the living types. This implies that the presence of seeds does not necessarily imply a genetic relationship.

CHAPTER V

BRYOPHYTA—CLASS I. ANTHOCEROTES

The Anthocerotes include but a single family, Anthocerotaceae, with about 300 species. The family is a very natural one, but its relationships with the other archegoniates are by no means clear; and it is an open question whether the differences between the Anthocerotaceae and the other liverworts are sufficient to warrant the establishment of a special class, coordinate with the Hepaticae and Musci, or true mosses. We believe the recognition of the Anthocerotes as a class is warranted, but in any case the relationships between them and the other liverworts, the Hepaticae, are very uncertain.

The essential characters of the Anthocerotaceae are very uniform, and there is no question about their being closely related. They are distributed over all the warmer parts of the world. Four genera, Anthoceros, Megaceros, Dendroceros, and Notothylas, may be recognized. The largest genus, Anthoceros, has been subdivided but basis for doing so is not very clear. Stephani separates 55 species to form the genus Aspiromitus. Some of these, e.g., Aspiromitus vesiculosus, have an elongated thallus with marginal leaf-like lobes and elaters longer than in most species of Anthoceros; but the differences seem insufficiently constant to warrant the establishment of a new genus.

The gametophyte of the *Anthocerotaceae* resembles more nearly the algal Ulothricales than does that of any of the Hepaticae, and may be regarded as most resembling the algal ancestors of the archegoniates.

The gametophyte is a prostrate thallus composed of nearly uniform cells, each containing in most cases a single chloroplast much like that of the Ulothricales and often having a similar conspicuous pyrenoid. This type of chloroplast is unknown elsewhere among the archegoniates. The very simple gametophyte, together with the structure of the sex organs, offers some significant resemblances to the more primitive pteridophytes.

On the other hand, the sporophyte is much better developed than that of any of the Hepaticae and is in some respects comparable to that of the true mosses (Musci) or even to the lowest pteridophytes. Thus the Anthocerotes may be said to constitute a synthetic and presumably ancient group, with possible relationships on one hand with the bryophytes and the pteridophytes and on the other with the green algae.

In most species of Anthoceros, Megaceros, and Notothylas the game-

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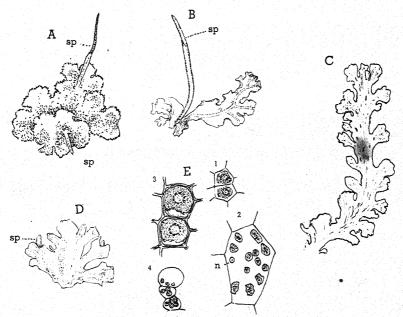


Fig. 34.—A, Megaceros tjibodensis; sp., sporophytes; B, Dendroceros Breutelii; C. Anthoceros vesiculosus; D, Notothylas orbicularis; E, chromatophores; E, 1, 2, from Megaceros; E, 3, from Coleochaete; E, 4, from Targionia.

tophyte is a somewhat fleshy, smooth thallus, branching dichotomously. More rarely it is elongated and ribbon-like, and may show marginal leaf-like lobes, e.g., Anthoceros vesiculosus. In Dendroceros the narrow elongated thallus has a thickened midrib and narrow wings composed of a single layer of cells. Most commonly the thallus is solid, but in some species of Antheroceros and Dendroceros, e.g., A. fusiformis and D. Javanicus, there are large intercellular spaces containing mucilage.

In all the Anthocerotaceae, colonies of blue-green algae (Nostoc sp.) are found. The Nostoc enters the thallus through clefts on the ventral surface, sometimes stoma-like in form. The universal occurrence of the Nostoc in the thallus indicates a true case of symbiosis.

The growth of the gametophyte is from a definite apical cell and is very much like that in the Hepaticae.

CHLOROPLASTS

While as a rule only one chloroplast is found in a cell, there are some notable exceptions. In *Anthoceros Pearsoni* there are usually two in each of the inner cells of the gametophyte, and in *A. Howellii* there may be four. In *Megaceros* there are from two to four in the superficial cells and some-

times as many as twelve in the large inner cells. In the latter case the chromatophores are round or oval, much like those of the typical green plant cell, and have no pyrenoid. Where the pyrenoid is present it may be very much like that of the algae, but more often it is composed of several irregular small granules.

GAMETANGIA

The gametangia of the Anthocerotes differ in some ways from the other bryophytes, and suggest rather those of the more primitive pteridophytes.

The antheridium, instead of arising directly from a superficial cell, is endogenous, i.e., is formed from the inner of two cells formed by a transverse wall in a superficial cell of the thallus. The antheridium thus lies in a closed cavity. In some cases, e.g., Dendroceros and Megaceros, the inner cell develops at once into an antheridium; in Notothylas and most

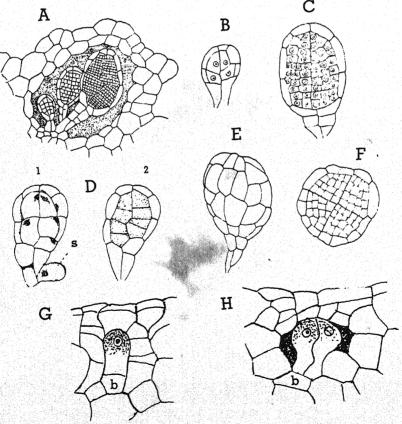


Fig. 35.-A-F, antheridia of Anthoceros fusiformis; G, H, young antheridia of Megaceros.

species of Anthoceros the primary antheridial cell divides by two intersecting vertical divisions into four cells, each of which becomes an antheridium. Sometimes secondary antheridia may arise by budding from the base of the primary ones. The first divisions in the young antheridium, whether derived directly from the primary antheridial cell, or from each of the four cells arising from its division, are the same. The two primary vertical walls are followed by transverse walls separating the stalk, or pedicel, from the body of the antheridium. A second series of transverse walls divides the body of the antheridium into similar octants, each of which soon divides into a peripheral cell and a central one, the latter dividing rapidly into the numerous spermatocytes, each of which develops a

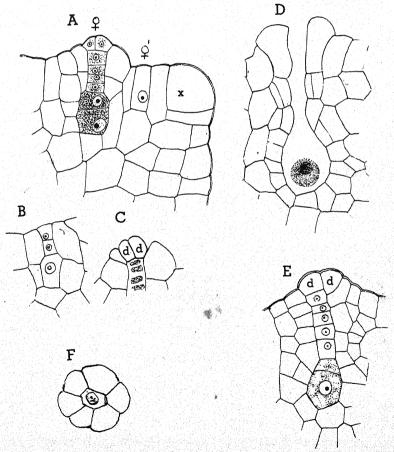


Fig. 36.—A-D, archegonia of Anthoceros fusiformis; d, cover cells; E, archegonium of Dendroceros Breutelii; F, cross section of archegonium of Megaceros.

single small biciliate spermatozoid. The wall of the antheridium is composed of a single layer of cells, each containing a conspicuous chromatophore which sometimes develops a conspicuous orange red pigment (haematochrome). The development of the spermatozoids seems to be much like that of other bryophytes.

The stalk of the antheridium may be short, but sometimes, e.g., in *Dendroceros*, it becomes greatly elongated and coiled up in the antheridial chamber. The outer wall of the antheridial chamber is composed of two cell layers.

ARCHEGONIUM

Except for the apex, the archegonium is completely embedded in the tissue of the gametophyte. The early stages are very inconspicuous and not easily recognized. Cross sections show an axial cell which has been formed by three intersecting walls in the mother cell of the archegonium. The axial cell is next divided by a transverse wall into an outer and an inner cell. From the first by a similar division a terminal, or cap cell, is separated from the primary neck canal cell. The inner cell is later divided into two nearly equal cells—egg cell and ventral canal cell. The primary neck canal cell divides into four or five, and the cap, or cover cell, may remain undivided, or may form two to four cap cells.

Of the four genera, Notothylas has the canal cells relatively broadest and Anthoceros the narrowest.

THE SPOROPHYTE

The early development of the sporophyte is much the same in all the Anthocerotes. The first division of the zygote is vertical, and this is followed by transverse walls in each cell. The four cells thus formed may be equal in size or the lower ones may be smaller. Each quadrant next is divided by a vertical wall into equal parts, and this octant division is followed by transverse walls in the upper octants, so that the embryo consists of three tiers of four cells each.

The next divisions are somewhat variable but always result in the separation of a central mass of tissue, the "endothecium," and an outer region, the "amphithecium." Of the three primary tiers of cells the two lower form the foot, at least in *Anthoceros*.

A longitudinal section of the embryo at this stage shows already the somewhat conical form of the apical region and the broad foot, some of whose cells may begin to extend into root-like processes which penetrate between the cells of the gametophyte. A cross section of the apical region shows four central endothecial cells, surrounded by a single row of amphithecial ones.

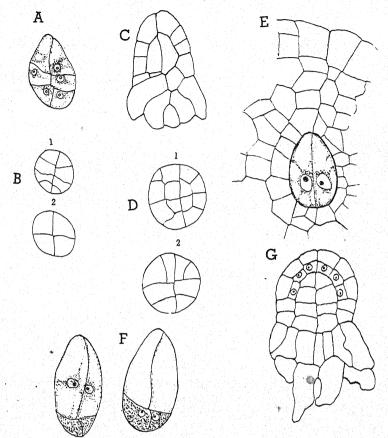


Fig. 37.—A, C, longitudinal, B, D, cross sections of young embryos of Anthoceros Pearsoni; E, two-celled embryo of A. fusiformis; F, four-celled embryo of the same; G, embryo of A. Pearsoni showing the archesporium.

The sporogenous tissue (archesporium) is very characteristic. Instead of arising from the endothecium, as is the case in most of the bryophytes, a series of periclinal walls in the amphithecium cuts off a layer of cells adjoining the endothecium and, seen in longitudinal section, shows a horse-shoe-shaped row of cells enclosing the upper part of the endothecium, the latter being denominated the "columella." Up to this point, except for some species of *Notothylas*, all the Anthocerotaceae agree in the structure of the embryo.

The young sporophyte soon shows three distinct regions: the apical region containing the sporogenous tissue, or archesporium; an intermediate zone of actively dividing cells; and the large foot. The subsequent growth is mainly due to the activity of the meristematic zone, and as a result of the

rapid cell division the older tissues are pushed up and the sporophyte may become greatly elongated.

The cell walls in the meristem correspond exactly, in position, with those in the young embryo, and the fully formed tissues of the upper part of the sporophyte merge gradually into those of the meristematic tissue above the foot; the developing tissues can be easily traced from the basal meristem to the ripe spores at the apex of the capsule. The foot grows rapidly and reaches its full size early in the growth of the sporophyte.

In most species of Anthoceros the original four rows of cells in the endothecium increase to sixteen, and the amphithecial cells outside the archesporium form three or four layers, of which the outermost is a well-marked epidermis provided with stomata closely resembling those of the vascular plants. Sometimes, according to Bartlett, the layer of cells next the archesporium has the character of an endodermis. The rest of the amphithecial tissue is composed of chlorophyllous cells, constituting an efficient apparatus for photosynthesis.

In most species of Anthoceros the archesporium is a single layer of cells in close contact with the columella in the younger parts of the sporophyte. In the meristematic zone the archesporial cells are hardly distinguishable except for their position; but higher up they show denser, more granular contents, and stain more readily than the neighboring cells. Finally they are differentiated into sporogenous and sterile cells, which sometimes show a pretty regular alternation. Each sporogenous cell is a spore mother cell, and forms a characteristic spore tetrad. The sterile cells remain undivided and increase in length, and are often united in chains. The spore mother cells and the sterile archesporial cells become isolated by the dissolution of the outer portion of the cell walls, and a large lacuna is then formed between the columella and the amphithecium, the spore mother cells lying free in this space. The columella later dries up and appears as a slender filament which protrudes from the open sporogonium.

The spore mother cell has a thin parietal layer of cytoplasm within which is a nucleus and a single chromatophore. The chromatophore divides twice and the four chromatophores and the nucleus are suspended. Following the division of the nucleus into four, and the formation of the spore tetrad, each spore receives one of the chromatophores.

When the first spores are ripe, the apex of the sporophyte ("sporogonium") splits into two valves, which separate gradually with the progressive ripening of the spores, toward the base of the sporogonium.

ANTHOCEROS

About two-thirds of the Anthocerotaceae belong to Anthoceros. The genus falls into two groups—those with yellow spores, and those with

black spores. A recent comparative study of the Anthocerotaceae by Bartlett shows that these characters are associated with other notable morphological differences, both of the gametophyte and sporophyte, in the two groups. In the black-spored species, e.g., A. fusiformis, the gametophyte is much more irregular in outline, with large mucilage-filled intercellular spaces; while in the yellow-spored forms, e.g., A. laevis, no lacunae are present and the mucilage is contained in special enlarged cells. The foot of the young sporophyte in the black-spored forms does not develop the rhizoid-like extensions of the superficial cells found in the yellow-spored species, but the surface of the foot is composed of a very definite epithelial-like layer of cells. There is a difference also in the form of the valves in dehiscence. In the yellow-spored forms they are usually twisted; in the black-spored species they remain flat. The sheath or involucre surrounding the base of the sporophyte is much better developed in the black-spored species.

In Anthoceros Pearsoni, a yellow-spored species, the archesporium is composed of two layers of cells; and in another species of the same group, A. Hallii, there may be as many as four layers of archesporial cells. The sterile cells of the archesporium are loosely united into a sort of network, which breaks up into fragments of varying size. There is a good

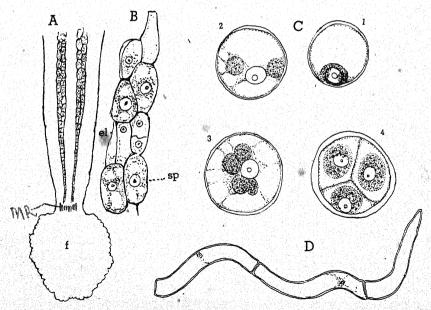


Fig. 38.—Anthocoros Pearsoni. A, basal region of sporophyte, showing the foot and archesporial tissue; B, archesporial tissue showing segregation of fertile, sp, and sterile, el, cells; C, spore division; D, elater of A. fusiformis.

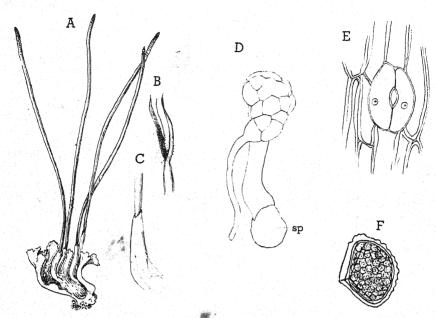


Fig. 39.—A, Anthocoros fusiformis, with four sporophytes; B, dehiscence of the ripe sporophyte; C, base of sporophyte, with surrounding sheath; D, young gametophyte of A. fusiformis; E, F, A. Pearsoni; E, stoma from sporophyte; F, ripe spore.

deal of variation in the lengths of the individual cells in different species. These "elaters" in *Anthoceros* never show the characteristic spiral thickenings of the liverwort elaters.

MEGACEROS

Megaceros includes a considerable number of mainly tropical species closely resembling Anthoceros in general appearance and in many cases originally placed in that genus. There are, however, some marked differences. The cells of the gametophyte always contain several chloroplasts, and the antheridia are solitary. The sporophyte which may reach a large size has no stomata in the epidermis, and the ripe spores contain chlorophyll, which is absent in all species of Anthoceros. The sporogenous tissue is much more abundant, the archesporium is composed of three to four layers, and there is a marked increase in the sporogenous tissue above the apex of the columella, suggesting the condition in Notothylas. While the archesporium in Megaceros differs thus from that in most species of Anthoceros, A. Pearsoni and A. Hallii, in the increased development of the archesporium, are intermediate between Megaceros and the typical Anthoceros. While the elaters in Megaceros resemble in form those of Anthoceros, they are provided with thickened spiral bands, recalling those of the Hepaticae.

DENDROCEROS

The species of *Dendroceros* are, like *Megaceros*, mainly tropical, and are epiphytic in habit. The gametophyte has a conspicuous thickened midrib upon which are borne the gametangia, which are solitary as in *Megaceros*. The marginal wings of the thallus are unistratose. The development of the sporophyte in the early stages is much like *Anthoceros*, but it is smaller. As in *Anthoceros* there is but a single layer of archesporial cells, except immediately above the apex of the columella; but it is more like *Megaceros* in the absence of stomata and in having elaters with spiral thickenings. The spores are much larger than those of the other genera. They contain chlorophyll, like those of *Megaceros*, and in some species begin germination while still within the sporogonium.

NOTOTHYLAS

Notothylas is much smaller as to both the gametophyte and the sporophyte. Most of the species are tropical, but N. orbicularis occurs in eastern United States.

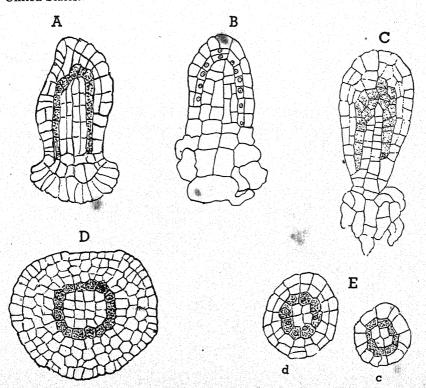


Fig. 40.—Embryos of Anthocerotes. A, Anthoceros fusiformis (after Bartlett); B, Megaceros tjibodensis; C, Notothylas javanicus; D, cross section of sporophyte of A. fusiformis; E, two cross sections near the base of the capsule of Notothylas javanicus.

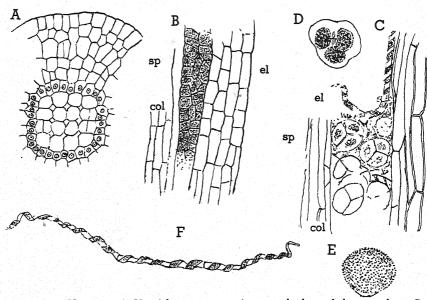


Fig. 41.—Megaceros. A, M. salakensis, cross section near the base of the sporophyte; B, longitudinal section in an older part in M. tjibodensis, showing the archesporial tissue; D, spore mother cell undergoing first nuclear division; C, spore tetrads and elaters; E, ripe spore of M. salakensis; F, elater of M. tjibodensis.

There is here a much greater development, relatively, of the sporogenous tissue. The foot is relatively small and the activity of the basal meristem ceases much earlier than in the other genera, so that the ripe capsule is but little elongated. There is a good deal of difference in the development of the sporophyte in different species. In *N. orbicularis* the early development is very much like that of *Anthoceros* and the sporogenous tissue arises exclusively from the amphithecium; but in some other species part at least of the sporogenous tissue is derived from the endothecium and no definite columella is formed.

Goebel states that in N. flabellata the sporangial tissue is formed exclusively from the endothecium and that although there is cut off from the amphithecium a layer of cells corresponding to the archesporium of the other forms, these cells are sterile, forming a "tapetum." As Goebel's material was obtained from dried herbarium specimens and was not sectioned, his conclusions must be accepted with some reservation. In N. Javanicus, there is an intermediate condition. Sometimes in this species a well-marked columella is present, like that of N. orbicularis; but in some cases the columella is much smaller and the upper portion develops spores. In all species the archesporium occupies a much greater part of the sporogonium than it does in any of the other genera. The archesporium, where a colu-

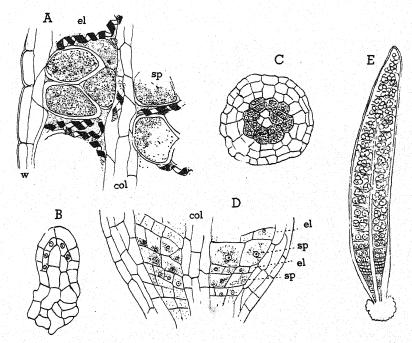


Fig. 42.—A, spores and elaters of *Dendroceros Breutelii*; B, young embryo of *Notothylas javanicus*; C, cross section of an older embryo; D, basal region showing the division of the archesporium into sterile and fertile layers; E, mature sporophyte of N. orbicularis.

mella is present, is about four cells thick and shows a regular alternation of fertile and sterile cells. Where no columella is developed, these alternating strata extend completely across the capsule except for the outer amphithecial tissue, which is much less developed than in the other genera. Very little chlorophyll is present, and stomata are wanting. The sterile cells (elaters) of the sporogenous region are short and irregular in form. They have short, curved, thickened bands in their walls—a condition intermediate between the definite spiral bands in Megaceros and Dendroceros and the smooth walls in Anthoceros.

COLUMELLA

The endothecium in all Anthocerotaceae forms an axial cylinder which in all except some species of *Notothylas* is sharply differentiated from the archesporium and forms the columella, which takes no part in spore formation. In the younger portion of the sporophyte the columella is in close contact with the archesporium and, it may be assumed, is concerned in the nutrition of its cells; but with the growth and isolation of the spore mother cells and elaters the columella is more or less completely separated

from the amphithecium, and in Anthoceros the lacuna so formed is very conspicuous and the columella is a slender filament lying free in the lacuna. In most species of Anthoceros the columella in cross section shows sixteen cells, very regularly arranged; but sometimes, e.g., in Megaceros and Anthoceros Hallii, the number may be considerably greater.

RELATIONSHIPS

Notothylas is undoubtedly the least-specialized member of the family; but whether this condition is primitive or secondary is a matter of debate. The increased development of the sporogenous tissue and the fact that sometimes the endothecium may contribute to it; the limited activity of the basal meristem; the small foot and subordination of the photosynthetic tissues, all suggest a possible relationship with some of the more primitive Hepaticae like Sphaerocarpus or Cyathodium, and it has been held that the Anthocerotes have been derived from Hepaticae. Admitting a real relationship between the two classes, it is quite as likely that the Anthocerotes are the older types, and the Hepaticae the derivative ones.

Notothylas, however, is regarded by some investigators, e.g., Lang and Bartlett, as a secondary form derived by reduction from the more highly specialized types like Anthoceros. A. Hallii resembles Notothylas in having a relatively small sporophyte and in increased development of sporogenous tissue. There is also a less-developed meristem and a much smaller foot than in the typical species of Anthoceros, with which, however, it agrees in having numerous stomata. Intermediate between A. Hallii and the typical species is A. Pearsoni, where the archesporium is regularly two-layered.

Megaceros has points of contact with all of the other genera. In the general form of the thallus and the very large sporophyte it resembles the most highly developed species of Anthoceros. The sporophyte, however, although the chlorophyllous tissue is abundant, lacks stomata and thus resembles Dendroceros, with which it also agrees in having chlorophyll in the ripe spores and elaters with conspicuous spiral bands. The sporogenous tissue is more extensive than in either typical species of Anthoceros or Dendroceros, and is rather suggestive of Notothylas. Since a similar increase of sporogenous tissue also occurs in Anthoceros Hallii and A. Pearsoni these would serve quite as well to connect Megaceros with Anthoceros. This applies also to the gametophyte of Anthoceros; for in both A. Pearsoni and A. Hallii there are regularly two chloroplasts in the cells instead of the single one found in most species of Anthoceros, Dendroceros, and Notothylas. A. Pearsoni also has solitary antheridia, agreeing thus with Megaceros and Dendroceros.

The multiple chloroplasts of Megaceros are much like those of the higher plants and may, perhaps, be considered as a condition intermediate

between the alga type found in most of the Anthocerotaceae and that of the other embryophytes. It is perhaps significant that in one of the simplest Hepaticae, Cyathodium, having a sporophyte quite suggestive of Notothylas, the chloroplasts are few in number and recall those of Megaceros. In none of the Hepaticae, however, is there any evidence of the amphithecial origin of the archesporium.

RELATION TO MUSCI

The true mosses, Musci, are the predominant bryophytes of the present and are highly specialized plants whose origins are not very clearly understood. The Sphagnaceae, or peat mosses, which differ much from the typical mosses, and are regarded as the most primitive family, show certain features which indicate a possible relation to the Anthocerotes. The embryo in Sphagnum resembles very closely corresponding stages in Anthoceros. Its early divisions are very much alike, and its archesporium is formed from the amphithecium, exactly as in Anthoceros. In the more specialized mosses, the sporogonium, like that of Anthoceros, shows a long-continued growth, the development of an elaborate photosynthetic apparatus, and a great reduction of the sporogenous tissue, which, however, is of endothecial origin. It is probable, however, that the highly specialized sporophyte of the higher mosses is a case of parallel development rather than an indication of any close relationship with Anthoceros.

The large almost independent sporophyte of Anthoceros, with its efficient photosynthetic tissue system and its long-continued growth, also invites comparison with the sporophyte of the lower pteridophytes. On the other hand, the extremely simple gametophyte may be compared with such algae as the Ulothricales.

Thus, in a sense, the Anthocerotes would seem to represent an ancient synthetic type with possible relationships to the archegoniates on the one hand and to the green algae on the other.

The evidence for real relationship between the Anthocerotes and the primitive pteridophytes is quite convincing. In Anthoceros the active growth of the sporophyte continues for several months and the sporogonium may reach a length of several centimeters. Spore production is subordinated to vegetative growth, and so long as the photosynthetic tissues are active and the water supply is maintained there is no inherent reason why the sporophyte should not continue to grow.

In the younger portions, where the archesporium is in close contact with the columella, the latter presumably acts as a water-conducting strand equivalent to a vascular bundle; but in the older parts, where the spore formation is advanced, the columella dries up. When the gametophyte dries up, the supply of water is cut off and the sporophyte necessarily dies.

In California the common species of Anthoceros remain dormant through the summer but revive promptly with the first autumn rains, and soon the development of the young sporophytes begins, to continue through the winter and spring, finally dying with the onset of the dry season.

The possibility of the survival of the sporophyte over the summer, when provided with moisture, was shown in a common Californian species, A. fusiformis. The sporophyte of this species normally reaches a length of about six centimeters but in some specimens collected in September near a stream where the gametophytes had not dried up, some of the sporophytes were still growing and had attained a length of sixteen centimeters.

An examination of these sporophytes showed not only a marked increase in length but in some of them the diameter was nearly double that of the normal sporophyte. The foot also was much enlarged, and in some cases, owing to the distintegration of the surrounding gametophytic tissues, seemed to have absorbed water directly from the substratum, thus practically establishing complete independence from the gametophyte comparable to that of a young fern.

These abnormal sporophytes also showed other marked changes. The sporogenous tissue in the younger parts was sometimes almost completely suppressed and in all cases the columella very much better developed than in the normal sporophyte and the amount of chlorophyllous tissue greatly increased. A section of such a sporophyte showed a massive central cylinder, comparable with the vascular bundle of some of the simpler pteridophytes. The lacuna surrounding the columella in the normal sporophyte was quite obliterated.

This essentially complete independence of the sporophyte brings up again the question of the possible derivation of the pteridophytes from forms similar to the Anthocerotes. In addition to the similarities in the gametangia of the Anthocerotes and the lower pteridophytes this demonstration of the ability of Anthoceros to develop efficient tissues, for both photosynthesis and water conduction, is a strong argument for the assumption of a real relationship between the Anthocerotes and some primitive pteridophytic type, and is a confirmation of the theory of antithetic alternation of generations in the pteridophytes.

The earliest known vascular plants are the Rhyniaceae, whose perfectly preserved remains were discovered in the Devonian rocks of Scotland.¹ These small leafless plants, which are of very simple structure, bear a remarkable resemblance in their anatomy to the large *Anthoceros* sporophytes just described. The main difference is the presence of tracheary

¹ R. Kidston and W. H. Lang, "Old Red Sandstone Plants from the Rhynie Chert," Trans. Roy. Soc. Edinb., 1-5: 1917-1921.

(woody) tissue in the axial bundle, a feature common to all "vascular" plants. These woody elements, however, are poorly developed in the Rhyniaceae and may be absent from some of the smaller shoots.

The Rhyniaceae also show an interesting resemblance to the Anthocerotaceae in their spore-bearing parts. The tips of some of the branches produce spores, and sections of these "sporangia" show the presence of a columella overarched by spores, much as in some of the Anthocerotes. All together these ancient vascular plants are very much what one might expect to find on the assumption that they were descended from some Anthoceros-like ancestors.

It has been argued by various students of the Anthocerotes (Leitgeb, Cavers, Goebel) that the sporophyte was derived probably from some form belonging to the Hepaticae. The sporophyte of Notothylas is compared with that of such simple liverworts as Sphaerocarpus, where the capsule is completely filled with sporogenous tissue. The columella is looked upon as a secondary structure comparable to the basal "elaterophore" in Pellia.

Notothylas, whether it is a primitive or a reduced type, does approach most nearly to the Hepaticae, although it must be said that the evidence for any but an extremely remote relationship between Anthocerotes and Hepaticae is not very convincing; and it is quite likely that the Hepaticae as a class are more recent than the Anthocerotes. While a comparison of the sporophyte of Notothylas with Sphaerocarpus has been proposed, perhaps a still greater resemblance might be found in Cyathodium. The very simple sporophyte of this liverwort has a foot with outgrowths recalling those of many Anthocerotaceae. Cyathodium and the related Targionia have much larger chloroplasts than is usual in Hepaticae and recall those of Megaceros.

APOSPORY

The sporophyte of Anthoceros has a marked power of regeneration of the tissues in case of injury. Pieces cut off and provided with the necessary conditions for growth may, from the cut surfaces, form cell masses which develop into thalli resembling normal gametophytes. This "apospory" was first shown by Lang, but the later, very detailed account is due to Marthe Schwarzenbach. She found in the young sporophyte that any of the cells were capable of regeneration, but that this was most marked in the meristematic zone, and in the subepidermal and sporogenous regions. The nuclei of the cells of the aposporous gametophytes are diploid.

CONCLUSION

Both the gametophyte and the sporophyte indicate that the Anthocerotes are very old types. It is quite conceivable that like the still more

ancient green algae, they are the little-changed descendants of plants which flourished long before the first vascular plants came into existence. We may fairly conclude that the ancestors of the first vascular plants, if not actually Anthocerotes, at any rate closely resembled them.

It is by no means improbable, also, that from the same stock were derived independently the Hepaticae and mosses, the two main divisions of the bryophytes. Of course the sporophyte of the primeval Anthocerotes must have been much simpler than in any living forms—perhaps comparable to that of such liverworts as *Riccia* or *Sphaerocarpus*.

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CHAPTER VI

HEPATICAE: SPHAEROCARPALES; MARCHANTIALES

The Anthocerotaceae, while probably related remotely to the other liverworts and usually associated with them in the class Hepaticae, differ so much in the structure of both gametophyte and sporophyte that their relegation to a separate class, Anthocerotes, seems warranted. The remaining liverworts show sufficient evidences of relationships among themselves to justify, for the present at least, their inclusion in a single class, Hepaticae.

While there is good reason to believe that some of the Hepaticae are very old types, little is known of their geological history and the few known Paleozoic fossils are referable to existing orders. Some of the living groups are well defined—e.g., Sphaerocarpales Ricciaceae—but the relationships of these groups to the others and the interrelationships of the members of the larger orders are not always evident; so that it can hardly be asserted that an entirely satisfactory classification of the Hepaticae has been established. Three orders—Sphaerocarpales, Marchantiales, and Jungermanniales—may be recognized, and possibly a fourth, Calobryales, might be added. Calobryum, the type of the Calobryaceae, usually placed in the Jungermanniales, differs essentially from the latter in the characters of both gametophyte and sporophyte.

THE GAMETOPHYTE

The gametophyte in the simplest Hepaticae closely resembles, superficially, that of the Anthocerotaceae. In certain species of Aneura (= Riccardia), Pellia, Sphaerocarpus, etc., it is a prostrate, undifferentiated thallus composed of uniform cells containing many small chloroplasts, instead of the single one characteristic of the Anthocerotaceae. It is true that Megaceros is to some extent intermediate in this respect between the Anthocerotaceae and the Hepaticae.

The growth of the gametophyte in the Hepaticae is due in most cases to the activity of a definite apical cell, and the branching is typically dichotomous. From the ventral surface of the prostrate thallus are developed delicate unicellular rhizoids.

From this primitive undifferentiated thallus there have been derived several more specialized types, evidently developed independently along several divergent lines of evolution. In *Sphaerocarpus*, for instance, the median part of the thallus forms a sort of indefinite midrib which merges

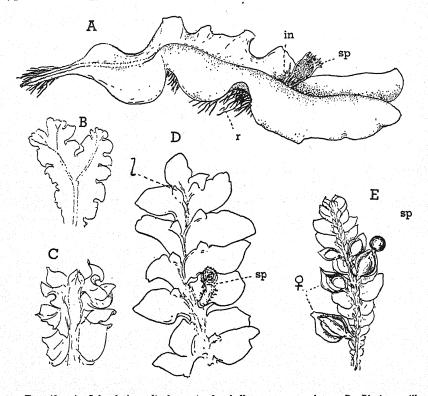


Fig. 43.—A, Calycularia radiculosa, simple thallus; sp. sporophyte; B, Blasia pusilla, thallus with marginal lobes; C, Fossombronia; D, Treubia, leaf-like marginal lobes; E, Porella, a "foliose" liverwort, with definite leaves; \$\partial 2\$, archegonial branch.

gradually into the thin marginal tissue composed of a single layer of cells. The same type occurs in some of the simple Jungermanniales, e.g., Calycularia and Mörkia; while in other somewhat more specialized forms like Pallavicinia and Podomitrium, placed by Cavers in separate families, there is a very sharply defined, thickened midrib, which may have an axial strand of elongated conducting cells, with thickened walls, recalling the tracheary tissue of the vascular plants. There is thus in these Hepaticae a certain division of labor, the midrib being primarily the water-conducting region, while the thin, expanded lateral wings composed of a single layer of chlorophyllous cells are special photosynthetic organs.

Differentiation of a somewhat different character is found in a number of the Jungermanniales. In these the basal portion of the gametophyte forms a prostrate cylindrical "rhizome," from which upright shoots arise which expand into green, leaf-like organs. In other cases, e.g., species of *Aneura*, the green shoots have a central axis from which spring much-

branched lateral shoots, the whole looking much like a finely divided fern frond. These leaf-like branches, like true leaves, are special organs for photosynthesis.

In another category are the leaf-like marginal lobes found in many Jungermanniales belonging to unrelated families and evidently developed independently. In their simplest form, the margin of the prostrate thallus shows a more or less marked lobing. Examples of this are Blasia pusilla and several species of Pallavicinia and Symphyogyna.

In the more specialized genera like *Treubia* and *Androcryphia*, these rather indefinite lobes become conspicuous leaves bearing a definite relation to the segments of the apical cell. Finally, the most specialized of the Jungermanniales, the Acrogynae or foliose liverworts, have very definite and sometimes quite complicated leaves. There are usually three definite rows of leaves, corresponding to three series of segments cut off from the tetrahedral apical cell.

The evolution of the gametophyte in the Marchantiales has been quite different. Here the thallose form has been retained but there is a marked specialization in the tissues, culminating in the higher Marchantiaceae. The green tissue is confined to the dorsal part of the thallus and is characterized by the presence of conspicuous air chambers or lacunae. In the lower forms, e.g., Riccia glauca, the lacunae begin as pits between the superficial cells near the growing point of the thallus. These pits develop into narrow air spaces between the vertical rows of green cells formed by the repeated transverse divisions in the superficial cells. The terminal cells of these rows are often much enlarged and probably regulate the opening and closing of the orifice of the narrow air chambers. In Riccia the dorsal green tissue merges gradually into the compact colorless ventral tissue.

In the more specialized genera, like Marchantia and Fegatella, there is a definite epidermis with characteristic pores communicating with a system of air chambers where the bulk of the green tissue is concentrated. There is a single layer of very definite chambers sharply set off from the solid, practically colorless tissue forming the ventral part of the thallus. The green tissue occupies the floor of the air chambers, and from it short filaments extend into its cavity. The cavity is roofed over by the epidermis, and there is a central pore, or stoma, opening into it.

There are two well-marked types of lacunae. In Fimbriaria californica, for example, with the growth of the thallus the lacunae, originating very much as in Riccia, become greatly enlarged and irregular in form, and the lacunar dorsal region of the thallus is not clearly deliminated from the solid ventral portion. This type occurs also in some species of Riccia and in a number of the less specialized Marchantiaceae.

In the more specialized genera, e.g., Marchantia and Fegatella, there is

a single tier of large air chambers, each opening by a single pore in the epidermis. This pore is surrounded by several concentric rows of epidermal cells, and in Marchantia and Preissia in the cells immediately surrounding the pore transverse walls occur so as to form a peculiar barrelshaped stoma, the innermost cells acting as guard cells. Similar stomata occur on the female receptacles of other genera, e.g., Fimbriaria and Reboulia.

The gametophyte of the Hepaticae has numerous rhizoids which in the Jungermanniales are alike but in the Marchantiales are of two kindslarge thin-walled, and smaller thick-walled, with characteristic peg-like outgrowths on the inner face of the cell wall. Glandular hairs and mem-

branous scales are present in many cases.

The spores of the Hepaticae on germination may form first an elongated "germ tube" at the apex of which the young gametophyte develops. Less often the first divisions in the germinating spore establish at once the growing point of the young thallus. In a few cases, e.g., Pellia and Fegatella, germination begins before the spores are shed. Less commonly a definite preliminary stage or "protonema" is developed from which the definitive gametophyte arises as a secondary bud. Examples of this are Protocephalozia, which has an alga-like protonema, and Metzgeriopses, where the protonema is a flat thallus, from which the leafy shoots arise as buds.

Gemmae.—Besides the vegetative reproduction through the separation of ordinary shoots or branches, special asexual reproductive bodies, gemmae, are found in many Hepaticae. These may be single cells, detached from the margin of unmodified leaves—a not unusual occurrence in some of the Acrogynae—or may be special multicellular bodies borne in special receptacles, e.g., Blasia pusilla, Lunularia, and Marchantia. In several species of Aneura, they are bicellular bodies formed within the cells of the thallus and discharged from these in much the same way as the motile zoöspores of many algae. Multicellular gemmae of endogenous origin have also been found in Metzgeria.

Tubers.—In a number of Hepaticae—and this also is the case in some species of Anthoceros-subterranean tubers are sometimes formed, especially in species which grow in regions with a marked dry season. In California such tubers are sometimes found in Fossombronia longiseta, and Goebel figures this in F. tuberifera, a Chilean species. Another Californian liverwort, Geothallus tuberosus, shows the same habit. The tubers in the latter remain dormant probably through several years, during long periods

Gametangia.—In the simplest Hepaticae, e.g., Sphaerocarpus and Ricof drought. cia, the sex organs are formed in acropetal succession, directly from dorsal superficial cells, and continue to form for a considerable period. In the

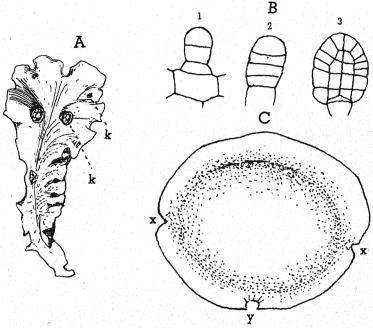


Fig. 44.—A, Marchantia polymorpha, with gemma-cups, k; B, development of the multicellular gemmae; C, gemma of Lunularia, showing two growing points, x, x.

majority of the genera, however, the gametangia are restricted to definite areas, and are often surrounded by a characteristic envelope or involucre. Not infrequently the fertile shoots are modified into special "receptacles," and a secondary envelope, or "perianth," may be formed inside the involucre.

In many cases the fertile branches are much reduced in size. These branches may replace the ordinary vegetative branches, e.g., the antheridial branches in *Aneura* or *Porella*; or they may be adventitious shoots, like the antheridial branches in *Targionia* and *Podomitrium*. The most specialized receptacles occur in the Marchantiaceae, where the female receptacle or "carpocephalum" is a branch system, resulting from the repeated and rapid dichotomy of the thallus apex.

The archegonium.—In general the Hepaticae agree in the structure of the archegonium. The primary neck canal cell divides into a row, varying in number, but the commonest number is eight. In the simplest types, e.g., Sphaerocarpus and Riccia, there are but four. Each of the three original peripheral cells may be divided by a radial wall, thus forming six peripheral cells, which by repeated cross walls form the six rows of

outer neck cells found in the lower Hepaticae, e.g., Sphaerocarpaceae and Marchantiales. In the Jungermanniales, much the largest order, however, one of the radial divisions is usually suppressed and there are typically but five rows of outer neck cells. Occasionally, e.g., in *Pallavicinia radiculosa*, there is a limited apical growth of the neck due to cells cut off from the primary cap cell, comparable to that found in the mosses.

The antheridium.—The antheridium of the Hepaticae is somewhat less uniform in structure than the archegonium. In the simplest forms, e.g., Sphaerocarpus, it develops from a papillate superficial cell which is cut off by a transverse wall. The first two divisions in the antheridium are transverse and of the three cells thus formed the lower one gives rise to the slender pedicel, the two upper to the capsule. The latter is divided by intersecting vertical walls into regular octants. Next are formed in each octant a periclinal wall, so that the body of the antheridium consists of eight peripheral and eight central cells. The latter, by repeated divisions, which are very regular, form the cubical spermatocytes, and the limits of the primary central cells are recognizable for a long time. The primary stalk cell, by a series of cross walls, forms the slender pedicel supporting the globular capsule.

In the Marchantiales, especially *Riccia*, the early development of the antheridium is much like that in *Sphaerocarpus*; but in the more specialized types the antheridium is much larger and the short pedicel thicker.

In the Jungermanniales the early divisions in the antheridium are somewhat different. The first wall in the body of the antheridium is a medium vertical one and in each of the resulting cells is followed by two walls which intersect each other and also the median wall. A cross section of the antheridium at this stage shows two central cells and four parietal ones. The pedicel is often much elongated, this being especially the case in the foliose species. In most of the Marchantiales the antheridia are borne in definite receptacles. These most commonly, e.g., Fimbriaria, Fegatella and Reboulia, are thickened discs, formed back of the apex. The receptacle shows conspicuous papillae, marking the cavities containing the antheridia. The antheridia are developed in acropetal succession from the apex of the thallus but do not interfere with its subsequent apical growth.

In the young antheridium a varying number of transverse divisions are formed before any vertical divisions appear, and the antheridium is more elongated than in *Sphaerocarpus* or *Riccia*. The separation of the peripheral and central cells takes place as in *Sphaerocarpus*; however, the lower segments do not form any sperm cells, but contribute to the massive pedicel. As in *Riccia* and *Sphaerocarpus*; the sperm cells are cubical in form and there is little displacement of the primary cell walls.

The final division of the spermatogenic cells results in a pair of sper-

matocytes, each of which develops into a spermatozoid. In *Marchantia* this division is diagonal and unaccompanied by any division wall, so that the two spermatocytes (spermatids) are triangular in section with the blepharoplast in the acute angle. This type of spermatid is probably typical for the Marchantiales.

The sporophyte.—As already noted, the simplest known sporophyte is that of Riccia, where except for a single layer of peripheral cells the whole sporophyte is made up of sporogenous tissue, all of whose cells give rise to spores. In all of the other Hepaticae there is a greater or lesser amount of sterile tissue. In the simpler forms like Sphaerocarpus and Corsinia there is a basal haustorium or "foot" and a globular capsule with a wall composed of a single layer of cells; some of the sporogenous cells remain undivided and form sterile cells, which, however, do not have the elongated form and spiral thickened bands characteristic of the "elaters" found in most of the Hepaticae. The sporophyte is best developed in the Jungermanniales, where there is usually a well-marked foot and a pedicel (seta), which, when the spores are ripe, may become greatly elongated and thus facilitates the distribution of the spores. The wall of the capsule has more than one layer of cells, and the dehiscence is very commonly by the splitting of the wall into four symmetrical valves; the elaters are elongated and have conspicuous spiral bands.

The sporophyte in all the Hepaticae has little chlorophyllous tissue and is, to a great extent, dependent upon the gametophyte for its nutrition, offering a marked contrast in this respect to the long-lived, nearly self-

supporting sporophyte of the Anthocerotaceae.

ORDER I. SPHAEROCARPALES

The Sphaerocarpales include what are, on the whole, the simplest and probably the most primitive of the Hepaticae. There are about twenty described species, belonging to two families, Sphaerocarpaceae and Riellaceae. To the first belong Sphaerocarpus, with seven species, and the monotypic Geothallus tuberosus, from southern California. The Riellaceae are represented by several species occurring in widely separated regions of the Old World and a single American representative.

Sphaerocarpus, the type of the order, and on the whole the simplest of the Hepaticae, has several species in the United States. The most widespread species is S. texanus (= S. californicus), abundant in California. The gametophyte, as already noted, is composed of uniform green cells, and under special conditions may develop leaf-like marginal lobes. The apex in the older plants shows several growing points resulting from the dichotomy of the primary apex. The plants are unisexual ("dioecious"), the females being very much larger than the males.

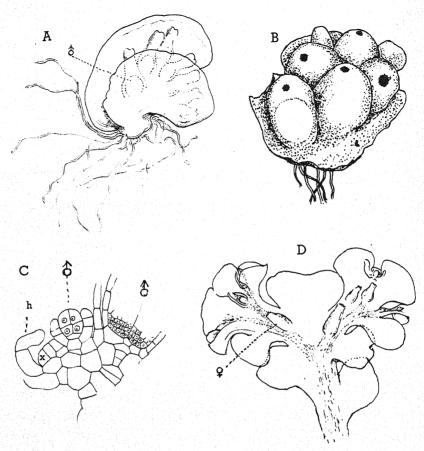


Fig. 45.—Sphaerocarpus. A, male plant of S. texanus; B, female plant of S. cristatus; C, apex of male plant, showing antheridia, σ ; D, female specimen, showing conspicuous marginal lobes.

The formation of the reproductive organs begins at a very early period and continues for an indefinite period, so that in the older plants the whole central portion is almost completely covered with the crowded and conspicuous involucres which surround the individual archegonia and antheridia.

The young gametangia arise close to the growing point of the thallus, from dorsal segments of the apical cell. Around each archegonium or antheridium the involucre begins to form at a very early stage of development. As already stated, the archegonium has four neck canal cells, and as in the Marchantiales there are six rows of parietal neck cells. The early stages of the antheridium also resemble the Marchantiales rather than the Jungermanniales.

The fertilized egg cell (zygote) is somewhat elongated, and the first division is transverse. Of the two cells thus formed, the upper (epibasal) gives rise to the capsule of the older sporophyte, the lower (hypobasal) to the conspicuous globular foot. In both epibasal and hypobasal regions another transverse wall follows, so that the young embryo is a short filament or cell row, a condition characteristic of most of the Jungermanniales but less marked in the Marchantiales.

In the older stages the globular foot is connected with the capsule by a short, narrow neck. The globular capsule has a wall composed of a single layer of parietal cells; and the central tissue, the archesporium, becomes differentiated into fertile and sterile cells, the latter remaining undivided and persisting as oval, thin-walled cells containing abundant chlorophyll and presumably contributing to the nutrition of the developing spore tetrads.

In most species of *Sphaerocarpus* the spores remain permanently united in tetrads. It has been shown by Allen that two of the spores produce male and two female gametophytes, and that there is a difference in the nuclei of the male and female spores, special sex chromosomes being present. In a common Californian species, *S. cristatus*, the spores separate completely.

Geothallus tuberosus is known only from southern California. At the

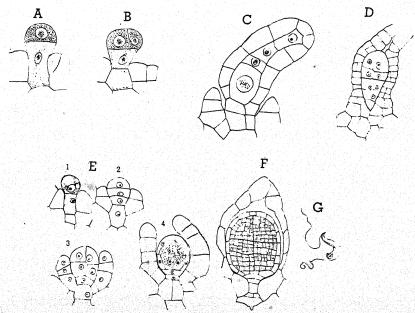


Fig. 46.—Sphaerocarpus. A, B, C, development of the archegonium; D, embryo; E, F, development of the antheridium; G, free spermatozoid.

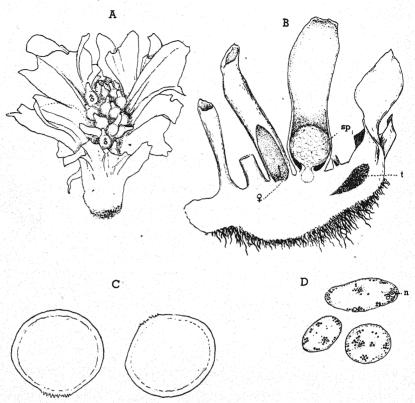


Fig. 47.—Geothallus tuberosus. A, male plant; B, section of female plant, with sporophyte, sp, and the beginning of the tuber, t; C, ripe spores; D, sterile cells.

end of the growing season it forms tubers which are buried in the soil and remain dormant for an indefinite period, germinating only when there is a heavier rainfall than is normal for San Diego, where it was discovered. It is much larger than Sphaerocarpus, which it resembles in the structure of the reproductive organs. The structure of the sporogonium is the same, except that the large spores are free. The gametophyte develops leaf-like lobes, and resembles that of Fossombronia, one of the lower Jungermanniales.

Riellaceae.—The second family, Riellaceae, includes about eight species of small aquatic plants, differing very much in appearance from any other Hepaticae. A single species, R. americana, is found in the United States, the others in South Africa, the Canary Islands, the Mediterranean regions, and Turkestan. All the species are submersed aquatics, having a cylindrical axis from which grows a dorsal thin lamina or wing, which may be somewhat spirally twisted. The reproductive organs are much like those

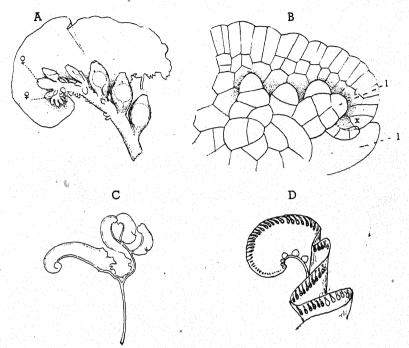


Fig. 48.—Riella. A, R. americana, apex of female plant; B, R. helicophylla, apical region; x, apical cell; l, leaves; C, R. americana, male plant; D, R. capensis, apex of male plant showing the antheridia (A, C, after Howe; B, after Leitgeb; D, after Cavers).

of Sphaerocarpus. The antheridia are formed along the margin of the lamina, the archegonia at its base where there are also small leaf-like appendages. The plants are dioecious.

ORDER II. MARCHANTIALES

The Marchantiales, with about four hundred species, form a very clearly defined order. Many of the genera and several species are cosmopolitan. Five families may be recognized—Ricciaceae, Corsiniaceae, Marchantiaceae, Targioniaceae, and Monocleaceae.

The gametophyte is always a prostrate thallus, commonly branching dichotomously, and there is no development of the leaf-like photosynthetic organs found in the more specialized Jungermanniales. Usually, however, the massive thallus, as already indicated, shows a marked specialization of the tissues. The ventral region is composed of compact tissue, with little or no chlorophyll; but there may be special secretory cells and sometimes mucilage sacs or even fibers. The green tissue is confined to the dorsal portion of the thallus and in the less specialized genera, like *Riccia*, there is a gradual transition from the green dorsal tissue to the colorless ventral

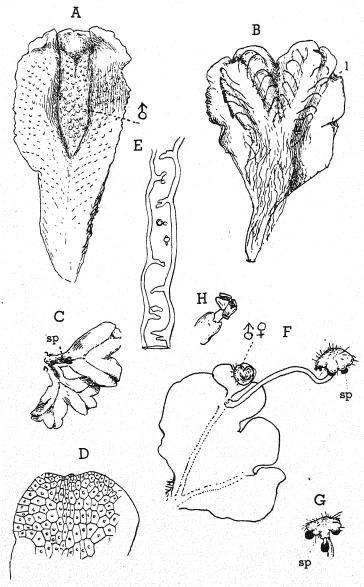


Fig. 49.—Marchantiales. A, male plant of Fimbriaria Californica; B, ventral surface of Fimbriaria; l, ventral lamellae; C, Riccia glauca; sp, sporophytes; D, Conocephalus conicus (Fegatella conica) showing the large air chambers and pores; E, tuberculate rhizoid of Marchantia; F, Dumortiera trichocephala; sp, the sporophytes; the receptacle c p bears both archegonia and antheridia; p, carpocephalum, with sporogonia; p, open capsule showing four valves.

tissue. In the dorsal region are formed the characteristic lacunae already referred to. These may be irregular in form—e.g., Riccia and Fimbriaria—or they may be the definite chambers found in the more specialized genera; e.g., Marchantia, Targionia, Monoselenium, Dumortiera, and Monoclea differ from the typical Marchantiales in having the thallus composed of uniform green tissue like that of the Anthocerotes. In Monoselenium and Monoclea there is no trace of air chambers, but in some forms of Dumortiera there are remains of dorsal lacunae which have become almost completely obliterated. It is generally assumed that these three genera have been derived from forms in which lacunae were present.

The rhizoids of the Marchantiales as already stated are of two sorts—large thin-walled and smaller thick-walled ones with spike-like protuberances on the inner face. There are also present membranaceous ventral scales, usually in two rows but in a few cases scattered. These arise near the apex of the thallus as small papillae, which may persist as the apex of the scale, e.g., Targionia; but more commonly the main portion of the complete scale is really a lateral appendage which pushes the original papilla to one side.

The apex of the thallus is occupied by a row of marginal cells which are much alike; it cannot always be shown that there is a single definite apical cell, but it is probable that this is the case. Seen in median longitudinal section, the apical cell is triangular in outline and from it are cut off in regular succession a series of dorsal and ventral segments. From the dorsal segments, by rapid growth and cell division, the major part of the thallus is derived. In *Riccia* the ventral segments divide only by vertical walls forming thin laminae which extend upward and protect the growing point of the thallus. With the lateral growth of the thallus these

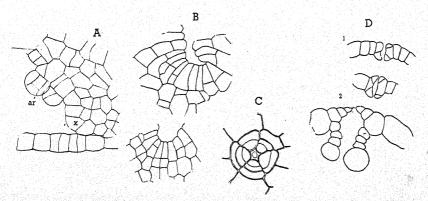


Fig. 50.—A, Targionia, apex of thallus; α , apical cell; αr , young archegonium; β , Riccia glauca, horizontal sections of thallus apex; C, surface view of pore from carpocephalum of Fimbriaria Californica; D, development of pore, in vertical section.

laminae in the older portions of the thallus are split and form two rows of overlapping scales. In the other Marchantiales the ventral segments of the apical cell contribute to the ventral part of the thallus and the scales are secondary outgrowths of the superficial ventral cells.

The branching is typically dichotomous; but sometimes, e.g., in Targionia, adventitious branches occur.

Gametangia.—In Riccia, the simplest member of the order, archegonia and antheridia are formed in most species on the same individual, are produced in acropetal succession for a long period, and are distributed over the dorsal surface of the gametophyte without any definite arrangement. In the Marchantiaceae they are restricted to a definite region and in the higher types are borne in characteristic receptacles.

In the Targioniaceae the archegonia are formed directly back of the apex of the shoot, exactly as in *Riccia*; but they are formed in rapid succession and only to a limited extent, so that a compact group is formed which is enclosed in an involucre composed of two large lateral lobes. The

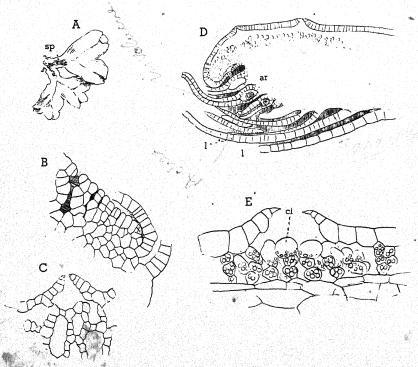


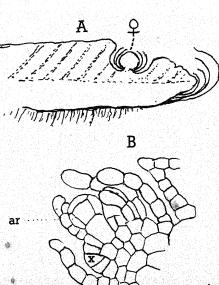
Fig. 51.—A, Riccia glauca; sp, sporogonia; B, section of growing point of Fimbriaria; x, apical cell; C, air chambers and pore of Fimbriaria; D, longitudinal section of thallus apex of Targionia showing archegonia, ar, and ventral scales, 1; E, air chamber and pore of Targionia; cl, chlorophyllous cells.

antheridia are borne on small adventitious branches arising from the ventral surface of the thallus.

In the Marchantiaceae, with few exceptions, the archegonial receptacle represents a much-modified branch system. This is also true of the antheridial receptacles in some of the most highly differentiated forms, especially the species of *Marchantia* and *Dumortiera*, where both antheridia and archegonia are borne on stalked receptacles which sometimes, e.g., the male receptacle of *Marchantia geminata*, shows very plainly the four branches resulting from the double dichotomy of the original short apex. In the familiar *M. polymorpha* the branches of the receptacle remain very short, and it forms a disc with eight growing points from which the groups of archegonia or antheridia arise. The female receptacle is known as a "carpocephalum," and its formation prevents any further growth of the shoot, as the original apex is involved in the growth of the carpocephalum.

Intermediate between the Ricciaceae and the Marchantiaceae is the small family Corsiniaceae, where the archegonia are formed in a group on the dorsal surface of the thallus but do not form a definite receptacle, although after fertilization a small elevation is developed upon which the sporophyte is borne. This may perhaps be the first indication of the carpocephalum of the Marchantiaceae.

Two genera of the Marchantiaceae, Clevea and Plagiochasma, may be said to connect the Corsiniaceae and Marchantiaceae as regards the struc-



ture of the carpocephalum. In these two genera the receptacle arises as a dorsal outgrowth close to the shoot apex, but not involving the apical cell, which continues to grow and divide, leaving the young carpocephalum free. Other younger ones may develop in a similar manner, so that two or more may occur upon the same branch. As the apex of the shoot is not involved in the further growth of the carpocephalum, the archegonia are developed independ-

Fig. 52.—A, Clevea sp., diagram showing dorsal origin of the carpocephalum; B, young carpocephalum of Reboulia; x, apical cell; ar, young archegonium (after Leitgeb).

ently. Three or four are formed around the margin of the young carpocephalum.

Since the development of the carpocephalum in the other Marchantiaceae involves the apex of the shoot, its formation stops any further growth of the branch, which can bear only a single carpocephalum. This may be illustrated by Fimbriaria (= Asterella). In F. californica the young carpocephalum shows clearly four growing points, evidently the result of a double dichotomy of the original growing point of the shoot. Each of these growing points develops a group of two or three archegonia surrounded by a conspicuous involucre. The growth of the dorsal tissue of the carpocephalum is excessive, so that the growing points are pushed downward and lie close to the stalk or pedicel of the receptacle. The cylindrical stalk is an extension of the axis of the thallus. The archegonia thus appear to be formed on the ventral surface of the carpocephalum, though morphologically they are dorsal structures.

After fertilization there is developed about each archegonium a special envelope, the "perianth," which keeps pace with the growing sporophyte. In *Fimbriaria* this perianth is a very conspicuous tubular sheath projecting from each of the four lobes of the receptacle corresponding to the four branches of which it is composed.

In the familiar *Marchantia polymorpha*, the compound character of the carpocephalum is emphasized by the development of the "middle lobe" between the eight apices of the receptacle. These lobes are much elongated and give the receptacle a stellate form.

Antheridia.—Except in the simplest types, i.e., most species of Riccia, the antheridia are developed in more or less definite receptacles. In the Marchantiaceae the antheridia are generally circular or oval cushions with papillate surface, the papillae marking the orifices of the chambers in which the antheridia are contained. The antheridia are formed in rapid succession from the apex of the shoot, and each antheridium is enclosed in a separate chamber formed by the tissue immediately surrounding it. After the formation of the receptacle is concluded, the apex of the shoot continues its normal growth and the receptacle is placed some distance from the apex of the shoot. Where the formation of a receptacle begins shortly before a dichotomy of the shoot apex, each new apex may continue to form antheridia and the receptacle is also forked. Only in a few genera, e.g., Marchantia and Preissia, is the male receptacle, like the carpocephalum, a compound structure borne on a pedicel. The antheridial receptacle in most species of Marchantia is a disc with scalloped edges, marking the growing points from which the antheridia extend in radiating rows. In M. geminata the receptacle is palmately divided into four branches.

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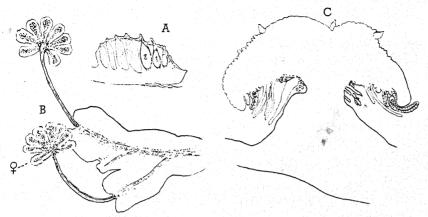


Fig. 53.—A, section of antheridial receptacle of Fimbriaria; B, Marchantia sp., with two carpocephala; C, section of young carpocephalum of Dumortiera trichocephala.

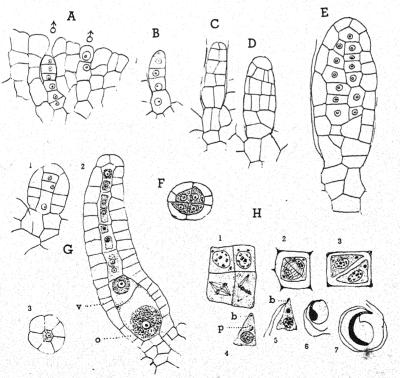


Fig. 54.—A-E, development of antheridium in Fimbriaria; F, cross section of young antheridium; G, archegonia of Targionia; G, 3, cross section of archegonium neck; H, spermatogenesis in Marchantia polymorpha (after Ikeno).

The sporophyte.—In none of the Marchantiales does the sporophyte attain a degree of specialization comparable to that of the gametophyte. In some of the genera, e.g., Marchantia and Riccia, the first two divisions of the zygote are at right angles and the globular embryo is divided into equal quadrants. This condition was supposed to be typical for the whole order; but more extended investigations, especially those of Meyer, have shown that in several genera, notably Plagiochasma, the young embryo

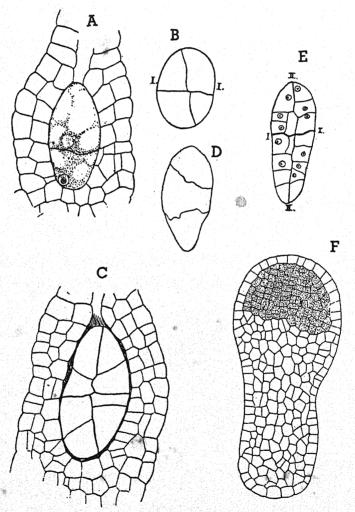


Fig. 55.—A, two-celled embryo of Targionia; B, four-celled embryo; C, an older stage; D, three-celled embryo of Dumortiera velutina; E, embryo of Fimbriaria; F, young sporogonium of Fimbriaria, the archesporium shaded.

consists of a short series of three or four cells, much like the embryo of Sphaerocarpus.

Meyer recognizes two types of embryo, the filamentous and quadrant, both including simple or primitive and highly differentiated forms. He believes the filamentous type is the primitive and the quadrant the secondary one. The filamentous type includes Plagiochasma, Grimaldia, Reboulia, Fegatella, and Fimbriaria, probably also Cryptomitrium and Cyathodium. In the quadrant type he places Marchantia, Preissia, Astroporae, Ricciaceae, and Corsiniaceae. In all of the Marchantiaceae the first division wall marks the separation of the epibasal sporogenous or capsular region from the hypobasal foot. In most of the Marchantiaceae the foot remains relatively small and the seta is slightly developed, the elongated pedicel of the carpocephalum serving the function of the elongated seta of the Jungermanniales in facilitating spore distribution.

In all of the Marchantiales the wall of the capsule is composed of a single layer of cells ("unistratose"), but there may be a more or less conspicuous "cap" at the apex composed of three or four layers of cells. This cap sometimes becomes detached, leaving a definite apical pore; but more often the capsule wall breaks irregularly. In Dumortiera and Wiesnerella it splits into several irregular "valves." The walls of the parietal cells may be uniformly thickened, as in Fimbriaria, or there may

be "ring-fibers" as in Marchantia and Dumortiera.

Of the five families of the Marchantiale—Ricciaceae, Corsíniaceae, Marchantiaceae, Targioniaceae, and Monocleaceae—the first three are evidently related and form an interesting series showing the progressive evolution of the sporogenous tissue. Differing in several respects from these three families are the two latter families, which probably represent two independent lines of development, originating near the base of the order; but it is not impossible that they have come from forms more nearly related to the Sphaerocarpales.

In Riccia all of the inner tissue (endothecium) is sporogenous and after the final division each cell normally develops a spore tetrad. In the Corsiniaceae the condition is much like that in Sphaerocarpus, i.e., a certain number of potentially sporogenous cells remain undivided and form thin-walled sterile cells, which, like those of Sphaerocarpus, presumably help to nourish the young spores. In Boschia (Funicularia), a related genus, the sterile cells develop irregular thickenings of the walls and may be called rudimentary elaters. In the Marchantiaceae the sterile cells become greatly elongated and develop the characteristic spiral bands of typical elaters. These are highly hygroscopic, and presumably facilitate the dehiscence of the ripe capsule and scattering of the spores.

CLASSIFICATION OF MARCHANTIALES

While the Marchantiales form a natural order, the interrelationships of the family are still somewhat uncertain. The three families, Ricciaceae, Corsiniaceae, and Marchantiaceae, form a natural sequence and possibly might be united into a single family; but the systematic position of the Targioniaceae and Monocleaceae is not so clear.

FAMILY 1. RICCIACEAE

The Ricciaceae, at least as to the sporophyte, are the simplest and probably the most primitive members of the order, although Goebel and some others, e.g., Meyer, believe that the simple sporophyte of *Riccia* is a case of reduction from that of some more specialized Marchantiaceae.

The family is a large one, comprising about one hundred fifty species, mostly species of *Riccia*, a cosmopolitan genus especially developed in countries with a well-marked dry season, like the Mediterranean regions and California. They often grow in exposed locations and are able to withstand long periods of drought without injury. They are less abundant in more humid regions, but there are a small number of true aquatic species, e.g., *R. natans*, *R. fluitans*. Both of these species, however, have terrestrial phases which were described as different species.

A second genus, Tessalina (Oxymitra), has the thallus, with a single tier of air chambers, each with a single pore, much as in the Marchantiaceae, and two rows of independent ventral scales. While the gametophyte approaches that of the lower Marchantiaceae, the sporophyte is a globular body like that of Riccia and all the sporogenous cells develop spore tetrads. The parietal layer of sterile cells is not very well defined, and it has been suggested (by Goebel) that these are probably to be considered not as forming the wall of the capsule but rather as nutritive in function; and he thinks that the sterile layer of cells in Riccia may also be so interpreted.

Through such forms as *Tessalina* and *Riccia natans*, which also have definite air chambers, the Ricciaceae may readily be connected with the Corsiniaceae and through the latter with the Marchantiaceae.

FAMILY 2. CORSINIACEAE

This family contains but two genera, Corsinia and Boschia, each with a single species. C. marchantioides belongs to the Mediterranean regions, while Boschia is known only from Brazil. The structure of the gametophyte resembles that of Tessalina. In Corsinia the ventral scales are irregularly distributed, as they are in Riccia natans; in Boschia they are in two definite rows. In Boschia the air chambers also contain green filaments like those in Targionia and some of the higher Marchantiaceae.

The reproductive organs are restricted to a limited region. The group

of archegonia occupies a depression in the dorsal surface of the thallus, suggesting the beginning of a definite receptacle. The antheridia form a row along the middle of the thallus like that in *Tessalina* and *Riccia natans*.

The development of the sporophyte in *Corsinia* has been very completely investigated by Meyer. The globular zygote is divided by the transverse basal wall, and the succeeding divisions are much like those in *Riccia*. The globular embryo soon becomes somewhat elongated and the hypobasal region develops a foot, while in the epibasal region, which increases rapidly in size, there is the separation of a definite parietal layer (amphithecium) from the endothecium, from which the sporogenous tissue is formed, and some of the sporogenous cells remain undivided and form sterile cells like those of *Sphaerocarpus*.

The development of the sporophyte in *Boschia* is imperfectly known; but the ripe sporogonium differs from *Corsinia* in the presence of U-shaped fibers on the walls of the parietal cells, and annular or spiral bands on the sterile cells, which may be called rudimentary elaters.

FAMILY 3. MARCHANTIACEAE

The Marchantiaceae include all the genera in which there is a definite carpocephalum. In all of them typical elaters are present. Leitgeb makes three sections of the family—Astroporae, Operculatae, and Compositae. While this is to some extent a natural division, Leitgeb's conclusions as to the morphology of the carpocephalum have required modification. Cavers has treated this subject at length in his admirable monograph on the interrelationships of the bryophytes. He showed that Leitgeb was incorrect in his assertion that in all of the Astroporae and Operculatae the carpocephalum had only a single growing point. The compound nature of the carpocephalum in Fimbriaria was demonstrated by the writer, and Abrams showed that this was true also of Cryptomitrium. Cavers concludes that in all the Marchantiaceae except Clevea and Plagiochasma the carpocephalum is compound.

Astroporae (Cavers).—Cavers includes in the Astroporae four genera—Clevea, Sauteria, Peltolepis, and Gollaniella. In all of these the ventral scales are in several series like Corsinia and have no appendages; and the air chambers are, except in the middle of the thallus, in a single layer but lack the free green filaments found in the air chambers of the more specialized Marchantiaceae. The pores are simple and surrounded by a circle of cells whose radial walls are usually thickened so that a surface view has a stellate appearance—hence the name of the section.

In some of the Astroporae, e.g., *Clevea*, the antheridia are scattered along the midrib of the thallus, recalling the Ricciaceae. In other cases, e.g., *Peltolepis*, there is a definite cushion-shaped receptacle like that in

the higher Marchantiaceae. It is evident that the Astroporae are the simplest members of the Marchantiaceae and the most nearly related to the Corsiniaceae.

The development of the carpocephalum in the Astroporae is not uniform. In Clevea the apex of the shoot is not involved and grows beyond the young receptacle, which thus appears as a dorsal outgrowth. More than one receptacle, therefore, may be formed on the same shoot. Four archegonia are usually formed, but these are formed independently of the shoot apex. Each archegonium is enclosed in a sheath (involucre) developed from the adjacent tissue. In the other genera the apex of the shoot is involved and there is probably a dichotomy of the apex so that the carpocephalum is of the "composite" type. The capsule wall has fibrous thickenings on the cell walls, in which it differs from that of the Operculatae.

Operculatae.—The Operculatae differ from the Astroporae in the structure of the thallus, which in most cases, e.g., Fimbriaria, has the dorsal region composed of a spongy green tissue with irregular air chambers separated by single layers of cells and the individual lacunae may be more or less completely divided by secondary partitions. This lacunar green tissue passes somewhat gradually into the compact ventral tissue. The upper chambers open by simple pores, surrounded by several concentric rings of epidermal cells. The ventral scales form two definite series and have conspicuous appendages. The cells of the capsule wall are uniformly thickened and there is a more or less definite cap, which may fall off as a lid or may be broken into several pieces, leaving the remainder of the capsule wall as a cup or more usually with a toothed margin.

The antheridium.—The antheridial receptacles are sessile, and sometimes are forked where there has been a dichotomy of the apex of the shoot. The development of the antheridium in Fimbriaria is much like that in Riccia, but the pedicel is thicker. There are several transverse divisions before any vertical walls are formed. As in Riccia the antheridium is sunk in a chamber, opening by a narrow canal (ostiole) at the surface of the thallus. Each spermatocyte gives rise to a pair of slender biciliate spermatozoids. The discharge of the spermatozoids may be very forcible. Peirce found that in Fimbriaria californica the spermatozoids, violently expelled through the nozzle-like ostioles, were thrown vertically more than fourteen centimeters.

The young embryo of Fimbriaria, while showing evidences of a quadrant division, soon becomes elongated and somewhat pear-shaped. The foot is not greatly enlarged and merges somewhat gradually into the seta. After the first divisions in the embryo it is impossible to detect any definite order in the cell division. As the capsule enlarges, the sporogenous tissue

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(archesporium) becomes recognizable, as the cell contents are somewhat denser, but the exact limits are difficult to determine. In the older stages it forms a nearly hemispherical mass occupying only about half of the capsule region and is bounded by a single layer of parietal cells forming the wall of the capsule. At the apex there are two to three cell layers forming the cap.

There is no definite arrangement of the fertile and sterile cells in the archesporium. The sterile cells elongate rapidly while the spore mother cells round off and develop the tetrads of spores. As the spores mature the thick cell wall is differentiated into three layers, the outer one (epispore) developing characteristic sculpturings. The elaters at first are elongated, thin-walled cells with uniform, finely granular contents. At a later stage a spiral band of cytoplasm is deposited on the wall, recalling the spiral chloroplast of *Spirogyra*. This is the beginning of the thick spiral band of the ripe elaters.

Fimbriaria (Asterella), Reboulia and several other genera are included in the Operculatae. One genus, Plagiochasma, included by Cavers in this group, differs in the structure of the carpocephalum, which like Clevea does not involve the apex of the shoot. Cavers believes that Plagiochasma is the lowest member of the group.

Compositae.—Since it is probable that all of the Operculatae except Plagiochasma have the composite type of carpocephalum, and there is no other character which is not shared with some member of Leitgeb's Compositae, it might perhaps be advisable to unite the Operculatae and the Compositae into a single subfamily.

In the more specialized genera the lacunae are in a single layer and the surface of the thallus shows a reticulate pattern, with a pore in each space. The green tissue forms a compact layer on the floor of each chamber and short filaments extend into the air space. The end cells of these filaments are often enlarged and sometimes pointed, e.g., Fegatella. The pores are in most cases like those of the Operculatae; but in three genera, Preissia, Marchantia, and Bucegia, they are the barrel-shaped stomata already referred to. The inner cells of the stoma are enlarged and act as guard cells. Stomata of this type occur on the carpocephala of other genera.

The compact ventral tissue contains little or no chlorophyll, but there are often special cells containing a characteristic "oil body;" and sometimes there are large mucilage sacs (Fegatella) which are sometimes in rows. Sclerotic fibers occur in Preissia and in some species of Marchantia.

The most marked departure from the typical thallus of the Marchantiales is found in *Dumortiera* and *Monoselenium*. About half a dozen species of *Dumortiera*, large liverworts, mostly tropical, are unmistakably

related to the higher Marchantiaceae in their reproductive structures, but the lacunae are either entirely absent or are more or less completely disorganized. In the latter case, e.g., D. velutina, the air chambers begin to develop in the usual way but fail to keep pace with the enlargement of the thallus, only the remains of the lateral walls of the chambers persisting. Papillate cells occupying the exposed surface of the open chamber are remnants of the chains of green cells formed in such genera as Marchantia or Fegatella. The species of Dumortiera grow in damp situations, often on wet rocks or similar conditions, and it is generally assumed that their thallus structure is an adaptation to their semiaquatic environment.

Differing much in habit from the other species is *D. calcicola*, a species collected by the writer in Borneo. This, as the name indicates, grows on limestone debris or over outcrops of limestone. It is much smaller and more delicate in texture than the other species, and in the fertile plants the receptacles are borne on very short heart-shaped shoots which are linked together, giving the appearance of a single elongated shoot with two rows of leaves.

Wiesnerella denudata is a monotypic species having a remarkable distribution. It is common in Hawaii but has also been found in Java, the Himalayan region, and Japan. It is especially interesting as it is unmistakably closely related to *Dumortiera* but also evidently connected with the typical Marchantiaceae, so that it may be said to connect the latter with the reduced *Dumortiera*.

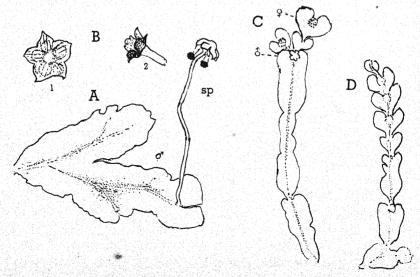


Fig. 56.—A, Wiesnerella denudata, &, antheridial receptacle; sp. sporogonium; B, dehiscence of capsule; C, D, Dumortiera calcicola.

Even more reduced in structure is the monotypic Monoselenium tenerum. This plant was first collected in northern India in 1849 by Griffith. It was rediscovered and described in detail by Goebel, the plants developing on earth with nursery stock sent from China to Munich. In 1923 the plant was found in California, apparently brought in with nursery stock from Japan or China.

In Monoselenium there is no trace of air chambers, and the sporophyte is also much reduced. According to Goebel the spores remain in tetrads and the sterile cells (elaters) contain chlorophyll, thus recalling Sphaerocarpus. In some cases there are imperfect spiral thickenings on the elaters. In general appearance, and in the character of the male and female receptacles, Monoselenium probably most nearly resembles Dumortiera, but shows a still greater degree of reduction.

Sporophyte.—The development of the sporophyte in the Compositae is much like that of the Operculatae, as illustrated by Fimbriaria. As in Fimbriaria, the amount of sporogenous tissue is relatively less than in Corsinia or Targionia, for example; but there is a more definite arrangement of the sporogenous and sterile cells than in Fimbriaria.

A recent paper by McNaughton describes in some detail the development in *Marchantia chenopoda*, and the writer's investigation of *Dumortiera* and *Wiesnerella* shows that these agree in most respects with *Marchantia*.

In Dumortiera velutina the zygote is somewhat elongated and the basal wall divides it into two cells, the epibasal one being the larger. The next wall is also transverse, so that the embryo is of the filamentous type. The three primary cells are divided into quadrants, but these divisions may be somewhat irregular. From the original hypobasal cell are developed the foot and part, at least, of the short seta. In the epibasal region the divisions are more regular and a series of periclinal walls separates the central region (endothecium), from which the sporogenous area, or archesporium, is formed, from the amphithecium, the wall of the capsule. The archesporium is somewhat limited in extent. The young sporophyte becomes oval- or pear-shaped in outline and the archesporium is recognizable as a broad band (in section) with a single layer of peripheral wall cells at the sides but with two or three layers at the apex-very much as in Fimbriaria. Whereas in the latter the cells of the archesporium are isodiametric, in Dumortiera (and Marchantia) the division walls are predominantly longitudinal and the cells, especially toward the center, are much elongated. Some of the cells remain undivided and become elaters; the others, by repeated transverse divisions, form rows of isodiametric cells, the young spore mother cells. The hypobasal region develops into a short seta and a not very well-defined foot.

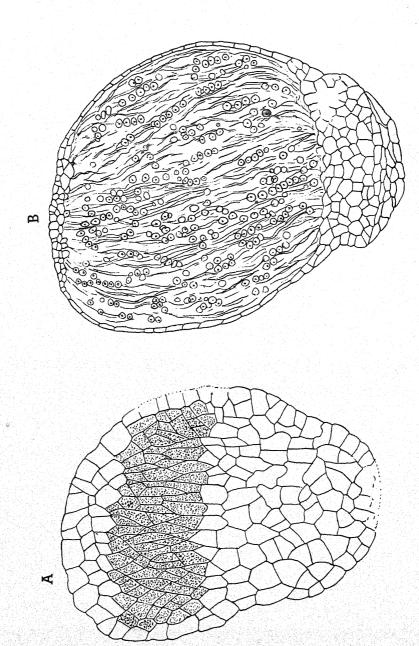


Fig. 51.—4, young sporogonium of Dumortiera trichocephala, the archesporium shaded; B, an older stage, showing young elaters and spores.

FAMILY 4. TARGIONIACEAE

The two families Targioniaceae and Monocleaceae differ in several respects from the Marchantiaceae and approach the lower members of the order. It has been suggested that the Targioniaceae are connected with the Ricciaceae through the Corsiniaceae, but it is not impossible that the Targioniaceae and Monocleaceae have arisen independently from types more like the Sphaerocarpales.

The Targioniaceae include two genera, Targionia and Cyathodium, with about eight species. The only species in the United States is Targionia hypophylla, common on the Pacific Coast but unknown in the Eastern states. The same species is found in Europe and in such remote regions as South Africa and Australia. In appearance it resembles many Marchantiaceae; but the thallus less often shows a regular dichotomy, and adventive branching is common. The anatomy of the thallus is like that of the higher Marchantiaceae. There is a single tier of air chambers with upright green filaments having enlarged terminal cells. There are two series of conspicuous ventral scales, and the rhizoids are typical.

The archegonia are formed in rapid succession from the growing point of the thallus, but no carpocephalum is formed. After the archegonial group is formed, the apical growth of the thallus ceases and the rapid enlargement of the dorsal tissues behind the archegonial group pushes these downward and there is developed about them an involucre composed of a pair of scales, which later increase greatly in size and completely enclose the developing sporophyte. The archegonium neck, which has eight neck canal cells, becomes greatly enlongated and bends upward, thus facilitating fertilization.

The antheridia are borne on small adventive shoots which arise from the flanks of the midrib on the ventral surface of the thallus. These antheridial branches extend to the margin of the thallus and the end forms a small flattened receptacle, the antheridia developing in acropetal succession, as in the Marchantiaceae, and their structure is essentially the same.

Sporophyte.—The zygote is somewhat elongated, and the first (basal) wall is transverse and separates the capsule region from the foot, as in most Marchantiales. In the Californian specimens studied by the writer the second divisions were vertical and the formation of regular octants, as in *Riccia*, seemed to be the rule. Miss O'Keefe, who studied material of supposedly the same species from Devonshire, describes the second division as also transverse, resulting in a three-celled filament like the embryo of *Sphaerocarpus* or *Plagiochasma*.

The further development agrees closely with that of the typical Marchantiaceae. The capsule wall is composed of a single layer of cells,

except at the apex, where it may be double. The parietal cells have conspicuous annular thickenings like those of the Astroporae.

A larger amount of the capsule region is devoted to spore formation than in the higher Marchantiaceae. In this respect *Targionia* recalls *Sphaerocarpus* and *Corsinia*. The archesporium shows no regular arrangement of the cells, the cells closely resembling each other until after the final division, where, like *Fimbriaria*, there can be distinguished two types mingled irregularly—isodiametric spore mother cells and somewhat elongated young elaters. By the partial disintegration of their cell walls they become separated. The spore mother cells increase rapidly in size and become distinctly four-lobed before the nucleus shows any signs of division. This lobing of the spore mother cell is typical for the Jungermanniales but does not occur in any of the Marchantiaceae.

Cyathodium includes about half a dozen species widely distributed in the humid tropics. The plant frequents shady places, sometimes shallow caves; and the delicate thallus seen from certain angles seems to emit a

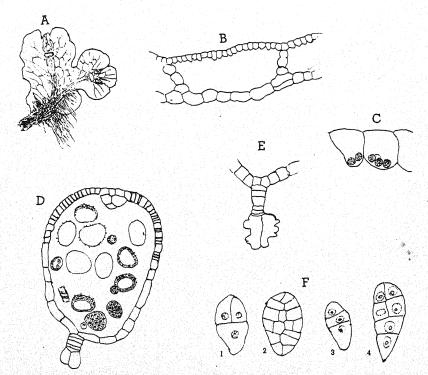


Fig. 58.—Cyathodium. A, ventral view of C. foetidissimum; B, section of the thallus; C, superficial cells with large chloroplasts; D, sporogonium of C. cavernarum; E, seta and foot, from a similar form; F, embryos; F, 1, 2, C. foetidissimum; F, 3, 4, C. cavernarum (C, D, E, F, after Lang).

greenish phosphorescence, apparently due to the reflection of light by the large chromatophores in the rounded superficial cells.

The largest and least reduced species, C. foetidissimum, is common in the Malayan regions and occurs also in Tahiti and probably in other parts of Polynesia. In this species the thallus consists of a single layer of air chambers bounded above by the epidermis, which has pores much like those of Targionia, and below by a single layer of ventral cells. In the median region the thallus is thicker, with an indefinite midrib. In the more reduced species, e.g., C. cavernarum and C. aureo-nitens, described by Lang, the air chambers are less definite and there are no tuberculate rhizoids such as are present in C. foetidissimum.

The position and structure of the gametangia are very like those of Targionia. The sporophyte in C. foetidissimum resembles that of Targionia, but in the more reduced species it recalls that of Sphaerocarpus. The first two divisions are transverse and the basal cells form a branched haustorium instead of the globular foot of Targionia. There is a short seta like that of Sphaerocarpus. True elaters, however, are formed.

Perhaps to be placed in the Targioniaceae is Aitchisoniella himalayensis (Kashyap), which resembles Targionia in the position of the archegonia; but the apex of the shoot may fork and two receptacles may be formed. These are somewhat constricted where they join the thallus.

FAMILY 5. MONOCLEACEAE

Among the largest of the Hepaticae are the two species of Monoclea, M. Forsteri of New Zealand and Patagonia and M. Gottschei in tropical America. The thallus of the former may reach a length of twenty centimeters, with a width of four centimeters or more. The thallus is dichotomously branched and resembles a very large Anthoceros or Aneura, the thick thallus being composed of practically uniform tissue. This resemblance to some of the anacrogynous Jungermanniales, and the fact that the sporophyte has a very long seta, has led some systematists, e.g., Schiffner, to place Monoclea in the Jungermanniales. However, the development of both gametangia and sporophyte, as shown by Johnson, indicates a nearer relationship to the Marchantiales, although it is possible that the family should be placed near the bottom of the series, perhaps close to where the two orders Jungermanniales and Marchantiales diverged from some parent stock.

In New Zealand, M. Forsteri often forms extensive mats in wet places or even in shallow streams where it is partly submersed. This marked hygrophilous habit might account for the complete absence of the lacunae characteristic of typical Marchantiales. Monoclea agrees with the latter in the presence of two kinds of rhizoids but has no ventral scales, these

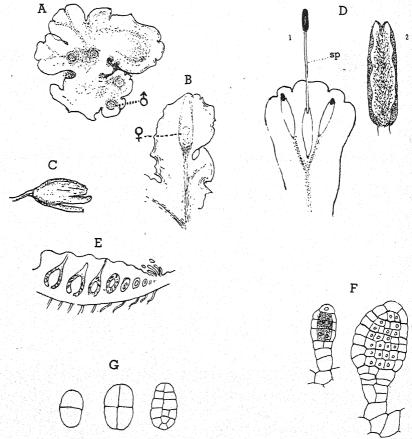


Fig. 59.—Monoclea. A, male plant of M. Gottscheii; B, archegonial receptacle containing young sporogonium; C, open capsule; D, M. Forsteri; D, 1, female receptacles and sporogonia; D, 2, open capsule; E, section of antheridial receptacle of M. Forsteri; F, young antheridia of M. Gottscheii; C, young embryos of M. Gottscheii (D, E, after Cavers; F, G, after Johnson).

being replaced near the growing point by hairs like those in Sphaerocarpus and many Jungermanniales.

The plants are dioecious. The antheridia resemble those of the Marchantiaceae and are borne in receptacles much like those of Fimbriaria or Fegatella. The archegonia are in a group back of the apex of the thallus, but no definite receptacle is formed and the formation of the sporophyte does not check the apical growth so that the sporophyte is not terminal. In this respect Monoclea might better be compared with Corsinia than with Targionia. A tubular involucre encloses the young sporophyte, and Cavers compares this with the involucre in Corsinia.

The early divisions of the embryo are like those in Corsinia or Mar-

chantia, and the wall of the capsule is unistratose as in the typical Marchantiales. As in *Targionia* the spore mother cells are deeply lobed before the first nuclear division and the ripe capsule is elevated on a very long seta like that in many Jungermanniales. It has been thought this character may be a response to the hygrophilous habit and the absence of a stalked carpocephalum.

Perhaps Monoclea bears somewhat the same relation to some of the lower members of the order, like Targionia or the Corsiniaceae, that

Dumortiera does to the higher Marchantiaceae.

Just as *Targionia* in its spore division suggests a possibly remote relationship with the Jungermanniales, so the Monocleaceae, in a sense, may be to some extent intermediate between the lower series of Marchantiales and the Jungermanniales.

CHAPTER VII

HEPATICAE: JUNGERMANNIALES; CALOBRYALES

A very large majority of the Hepaticae belong to the Jungermanniales. Out of a total of over 8,000 species, less than 500 belong to the Sphaero-carpales and the Marchantiales. While the Jungermanniales seem to represent a truly natural order the further classification is in a very unsettled condition and there is marked diversity of opinion as to the limits of the families and the genera included in them. The classification has been based largely upon external characters, and only a relatively small number of species have been critically studied as to their life history, and particularly the development of the sporophyte. Until much more has been done in this direction any classification proposed must, to a great extent, be merely tentative.

Cavers has published a careful and extended study of the classification which, while following Schiffner, differs in some important respects and has much to commend it. Cavers recognizes the difficulties in establishing a definitive classification and says: "The Jungermanniales form a single phylum, the boundaries between the systematic families, in most cases badly defined; and probably in no other group of plants do we find such striking and abundant examples of parallelism or homoplasy." More recently Goebel has proposed a classification of the Hepaticae which differs a good deal from Caver's arrangement.

The gametophyte of the Jungermanniales may be a simple thallus comparable to Anthoceros, while in the most specialized forms there is a definite axis bearing leaves which have a regular relation to the segments of the apical cell. Between these extremes there are many intermediate stages, and it is evident that very similar structures have arisen in several independent developmental lines. The tissues in most cases are very uniform and there is nothing comparable to the highly specialized tissues of the higher Marchantiaceae. In a few cases, e.g., Pallavicinia and Podomitrium, there is a definite strand of conducting tissue in the midrib of the thallus.

The sporophyte always consists of a definite capsule borne on an elongated seta, and often there is a well-defined foot. The capsule wall has two or more cell layers. Elaters are always present. Dehiscence of the capsule may be irregular, but more often the wall splits into four symmetrical valves.

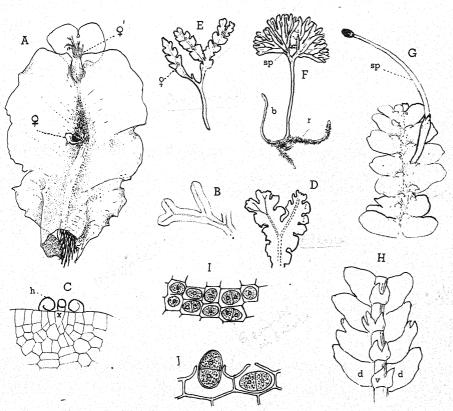


Fig. 60.—Evolution of gametophyte in Jungermanniales. A, Calycularia; B, Metzgeria; C, growing point of Metzgeria; D, Blasia; E, Symphyogyna; F, Umbraculum; G, Treubia; H, Calypogeia; I, J, gemmae in Aneura multifida (H, after Evans; I, J, after Cavers).

Before the first nuclear division in the spore mother cell the latter becomes strongly four-lobed, indicating the position of the four spores of the tetrad. The spore on germination usually develops a germ tube, at the apex of which the young thallus arises. The thallus may, however, develop directly. A definite protonemal stage is sometimes formed, the definitive gametophyte developing as a bud from it. In some tropical forms the protonema forms an extensive alga-like mass of filaments or a thallose protonema. The leafy shoot arises from the protonema as a special bud, much as in the true mosses.

The Jungermanniales fall into two pretty well-marked groups, "Anacrogynae" and "Acrogynae," based primarily upon the position of the archegonium; but this is a somewhat artificial distinction. In the Anacrogynae the archegonia are borne upon the dorsal surface of the usually

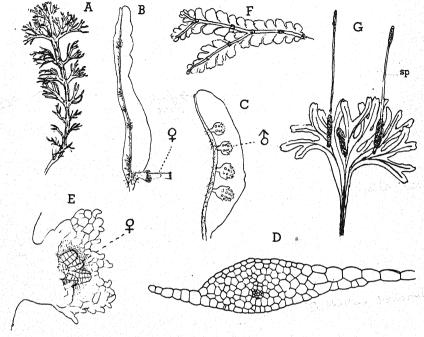


Fig. 61.—Types of Anacrogynae. A, Aneura sp.; B, female, C, male, gametophytes of Podomitrium malaccense; D, section of thallus of Podomitrium, showing central conducting strand; E, female receptacle of Aneura pinnatifida; F, Symphyogyna sp.; G, Pallavicinia (Mittenia) Zollingeri (G, from drawing by Miss Florence Williams).

prostrate shoot—much as in Sphaerocarpus or Riccia—and the further growth of the shoot is not interrupted. In the Acrogynae, which are foliose forms, the archegonia are borne at the apex of the shoot and finally the apical cell is transformed into an archegonium, which thus stops any further growth of the shoot.

The distinction between Anacrogynae and Acrogynae is by no means complete, as among the Anacrogynae are forms which closely approach the acrogynous condition and this is found in more than one family.

ANACROGYNAE

Cavers recognizes four families of Anacrogynae: (1) Codoniaceae; (2) Aneuraceae; (3) Blyttiaceae; and (4) Calobryaceae. The most recent attempt at classification is by Goebel, who recognizes five families: (1) Metzgeriaceae; (2) Pelliaceae; (3) Fossombroniaceae; (4) Treubiaceae; and (5) Calobryaceae. This will show the divergence of opinion by two competent investigators.

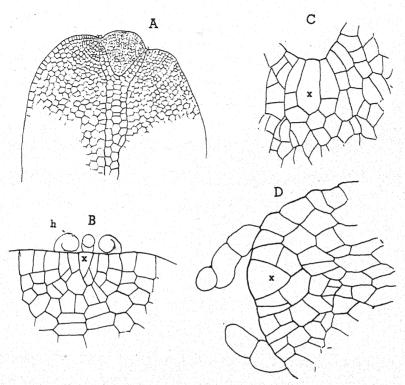


Fig. 62.—A, Metzgeria pubescens showing dichotomy; B, growing point of Metzgeria; C, D, Podomitrium malaccense, apical cell, x—C, in horizontal, D, in vertical section.

The Anacrogynae include something less than 600 described species. The simplest type of gametophyte—e.g., Pellia, Calycularia, and Aneura pinguis—is a simple prostrate thallus composed of practically uniform cells. In other genera, e.g., Metzgeria, Podomitrium, and Pallavicinia, there is a distinct midrib, with lateral wings composed of a single layer of cells and the midrib is traversed by a definite strand of elongated conducting cells. Such a thallus may show a basal rhizome-like region which expands gradually into the ribbon-like anterior portion. In some species of Pallavicinia (Mittenia) and in Umbraculum there is a cylindrical prostrate rhizome which develops an upright shoot, whose apex forks repeatedly into an expanded, fan-shaped "frond" which resembles strikingly the flabellate leaf of a filmy fern, the midribs of the segments of the "frond" simulating the vascular bundles of the fern leaf. A somewhat similar effect is seen in some species of Aneura; but in these there is no midrib, the branching is apparently monopodial—possibly the result of unequal

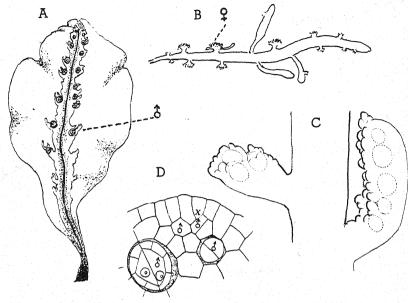


Fig. 63.—A, male thallus of *Pallavicinia Levierii* (from drawing by Miss Williams); B, Aneura pinnatifida with archegonial receptacles; C, two antheridial receptacles of the same; D, horizontal section of antheridial branch of Aneura.

dichotomy—and the finely divided lateral branches attached to the main axis have the appearance of a finely divided pinnate leaf.

Another modification is seen in the development of more or less definite marginal lobes. The simpler form is seen in *Blasia* and some species of *Symphyogyna*. This condition is comparable to that sometimes seen in *Sphaerocarpus*. Finally these lateral lobes assume a distinct leaf-like form, and are developed in definite succession, corresponding to the segments cut off from the apical cell. *Treubia* and *Androcryphia* represent this intermediate condition between the thallose Anacrogynae and the leafy Acrogynae, which are thus connected with the simpler Anacrogynae. It is not likely that the Acrogynae represent a single closed phylum, and it is quite conceivable that the existing Acrogynae have arisen from more than one line of Anacrogynae.

The gametophyte has a definite apical cell with very regular segmentation. In many Anacrogynae, e.g., Metzgeria and Aneura, two series of segments alternately right and left, are cut off from the apical cell. In Metzgeria the first division in each segment separates it into an outer and an inner cell. In the former only vertical divisions are formed and the cells contribute to the unistratose wings of the thallus. From the inner cells of the segments the thickened midrib is formed. The "two-sided"

apical cell is the commonest form in the Anacrogynae; but there is considerable variation, and in *Androcryphia* and *Treubia* a tetrahedral apical cell with three series of segments is found like that of the Acrogynae.

Gemmae.—Characteristic gemmae are found in some of the Anacrogynae. In some species of Aneura, bicellular gemmae occur which in their origin resemble the zoöspores of many green algae. The protoplast of a superficial cell contracts and secretes a new membrane. The cell then divides and the bicellular gemma is ejected much as a zoöspore would be. The gemma then develops into a new plant. A similar condition is found also in Metzgeria, but here the gemma forms a multicellular body before it is separated from the thallus. In Blasia pusilla special flask-shaped receptacles are formed within which globular gemmae are developed. These may germinate at once or may remain dormant for an indefinite period.

Gametangia.—In the less specialized genera the gametangia are somewhat irregularly disposed over the dorsal surface of the thallus, which may be bisexual or unisexual. In Fossombronia the gametangia are placed irregularly much as in Riccia or Sphaerocarpus. In the more specialized genera the gametangia are sometimes borne on special branches, developed either from the margin of the thallus (Aneura) or from the ventral surface attached to the midrib (Metzgeria, Podomitrium). In some cases the antheridia are arranged along the midrib on the dorsal surface of the thallus, protected by thin scales.

The first division in the mother cell of the antheridium is transverse. In Pallavicinia the lower of the two primary cells forms the short stalk of the antheridium and also a layer of cells separating the spermatogenous tissue from the base of the capsule. The outer of the two primary cells shows the typical divisions of the Jungermanniales; i.e., the first wall is a central median one, followed in each of the daughter cells by a nearly periclinal division which divides it into two very unequal cells. This wall intersects both the outer wall of the antheridial cell and the median one and is quickly followed by a similar wall which meets the first one and also the median wall. In cross section the antheridium shows two triangular central cells and four narrow parietal ones. This structure appears to be typical for the Jungermanniales; but Humphrey found in Fossombronia longiseta that the early divisions of the antheridium more nearly resembled those in Sphaerocarpus. Haupt states that he could not confirm this. The later divisions in the spermatogenic cells are much less regular than in the Marchantiales. The pedicel is short in all the Anacrogynae that have been examined.

Spermatogenesis.—Humphrey studied the development of the spermatozoids in Fossombronia, which differs somewhat from that of the typical Jungermanniales. The mother cell of the spermatozoids, as in the Marchan-

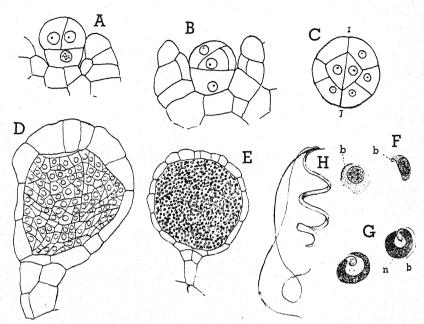


Fig. 64.—A, B, young antheridia of Podomitrium malaccense; C, cross section of young antheridium; D, E, antheridia of Calycularia radiculosa; F, young spermatocytes of Calycularia; b, blepharoplast; G, older stages; H, spermatozoid of Pellia (H, after Guignard).

tiales, divides diagonally; and there is no division wall formed between the two young spermatids, which in section appear triangular, with the blepharoplast at the acute angle. Owing to the large size of the spermatozoids in *Pellia* this has been the subject of numerous investigations; but the other genera investigated—*Calycularia*, *Aneura*, and *Pallavicinia*—differ from *Pellia* only in minor details. In all of these the mother cell of the spermatozoids is nearly globular and the final division is by a cell wall, completely separating the two spermatids. The development of the elongated coiled body of the spermatozoid from the nucleus, and the occurrence of the blepharoplast with the two cilia, are much alike in all of them (for details see chapter iii, p. 29).

The archegonium.—The structure of the archegonium is much the same in all the Anacrogynae; but there is some variation. Typically there are five rows of outer neck cells; but there may be exceptionally six in Fossombronia, and in Treubia there may be as many as nine. In some cases there is a limited apical growth in the archegonium neck. In Pallavicinia radiculosa the cap cell of the young archegonium sometimes has several lateral segments cut off before the final quadrant divisions are formed. The number of neck canal cells varies but is in most cases five

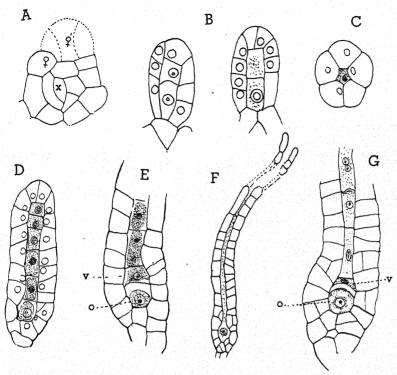


Fig. 65.—A, a young archegonial receptacle of Aneura pinnatifida; x, apical cell; \(\bar{Q}\), young archegonia; B, young archegonia of Podomitrium; C, cross section of archegonium neck; D-C, development of archegonium in Calycularia radiculosa.

or six. In Treubia Grün states there may be sixteen; the writer found but eight.

The embryo.—The embryo is enclosed in a conspicuous "calyptra" formed by the active growth of the archegonium venter. The calyptra may become greatly enlarged enclosing the young sporophyte until the capsule is mature and involves the tissues adjacent to the archegonium, so that the unfertilized archegonia are carried up by the basal growth of the calyptra and are found at its apex. A second envelope, the perianth outside the calyptra, is present in some genera, e.g., Podomitrium and Pallavicinia.

The first wall in the zygote is transverse, and in most of the Anacrogynae the lower (hypobasal) cell remains either undivided or divides only once or twice and does not contribute to the foot. In Fossombronia the hypobasal cell develops the foot as it does in Sphaerocarpus. The second division is also transverse and the embryo is a short three-celled filament. This is typical of the Jungermanniales as a whole.

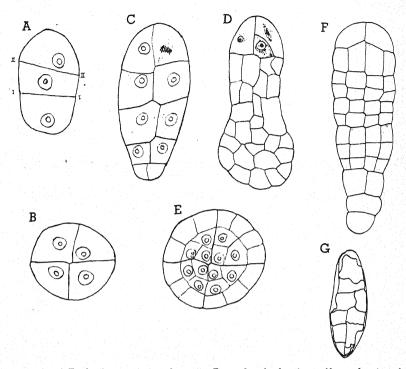


Fig. 66.—A-E, development of embryo in Fossombronia longiseta (from drawings by Dr. H. B. Humphrey); F, embryo of Aneura multifida; G, young embryo of Podomitrium (F, after Leitgeb).

The hypobasal cell becomes enlarged and forms a "suspensor," which may remain unicellular but more often divides into two or more cells and may function as a haustorium. Examples of this are species of Aneura and Pallavicinia. The further development of the sporophyte shows a good deal of variation. In Fossombronia the terminal cell is divided into four equal quadrants, in each of which a periclinal wall separates a parietal, or amphithecial, and an inner "endothecial" cell. The epibasal cells contribute to both capsule and seta. The capsule and foot increase rapidly in size and the dumbbell-shaped young sporophyte suggests that of Sphaerocarpus.

The parietal cells of the capsule divide by periclinals so that the capsule wall is two-layered. The sporogenous tissue (archesporium) is composed of uniform cells which later are differentiated into spore mother cells and elaters but show no definite relation to each other.

Except in Fossombronia, the foot, seta, and capsule are all of epibasal origin but there is a good deal of variation in the later divisions of the embryo and the relations of the different organs to each other. The sporophyte has a conspicuous seta which before the dehiscence of the

capsule elongates rapidly at the expense of the starch and other food material stored in its cells. There is an enormous elongation of the cells without any cell division. In *Pellia*, within three to four days the seta increased in length from 1 mm. to 80 mm. Sometimes, e.g., in *Pellia* and *Calycularia*, there is a conspicuous foot; but in other genera, like *Aneura* and *Pallavicinia*, the foot is not clearly differentiated and merges imperceptibly into the base of the seta.

The form of the capsule varies from perfectly globular in Fossombronia and Pellia to cylindrical in some species of Pallavicinia. In all cases it differs from the Sphaerocarpaceae and Marchantiales in having two or more cell layers in the wall. The apex of the capsule is often thicker and may form a conspicuous beak—e.g., Pallavicinia and Calycularia.

In Fossombronia the capsule is derived from the four quadrant cells of the terminal segment of the filamentous embryo—the seta from the intermediate segment and the foot from the hypobasal segment. Each of the terminal quadrants is next divided into an outer (amphithecial) and an inner (endothecial) cell. From the four primary endothecial cells the archesporium is derived. The capsule grows rapidly and the foot also enlarges, and the sporophyte at this stage may be compared with that of Sphaerocarpus; but the wall of the capsule becomes double, a conspicuous seta is formed, and typical elaters are developed.

The primary archesporial cells undergo rapid division and at first the cells are all quite uniform in appearance; but later there is a segregation into larger isodiametric cells—the young spore mother cells and smaller elongated ones, the elaters.

In Aneura the early development of the embryo, except for the hypobasal region, is much as in Fossombronia. The archesporium is formed in much the same way, but the differentiation of the archesporial tissues is quite different. A section of the young capsule shows that the endothecium is differentiated into an apical area of cells with less dense contents, these being enclosed laterally and below by a layer of rapidly dividing cells with denser contents. The latter give rise to the sporogenous tissue and elaters, while the rest of the endothecium remains sterile and forms the "elaterophore," which remains in contact with the wall of the capsule. With the rapid multiplication of the cells of the sporogenous region, the inner ones gradually lose their dense contents and add to the bulk of the elaterophore, only a thin layer of sporogenous tissue remains, and the spore mother cells and elaters are developed much as in Fossombronia; but the outer cells of the elaterophore grow out into elongated elaters-which remain attached to the elaterophore. The ripe capsule opens by four valves, each of which has a tuft of the fixed elaters at its tip, resulting from the splitting of the elaterophore.

In Pellia a similar elaterophore is formed at the base of the capsule and the fixed elaters form a dense tuft at the base of the open capsule.

The early stages of the embryo in Pallavicinia are like those in Aneura. but the divisions are somewhat less regular and the archesporium is not clearly differentiated until a later stage of development. In P. (Mittenia) Zollingeri, when the archesporial tissue is recognizable the capsule wall shows three layers of cells somewhat thicker at the apex. In vertical section the archesporium appears as a broad band of narrow cells arranged in

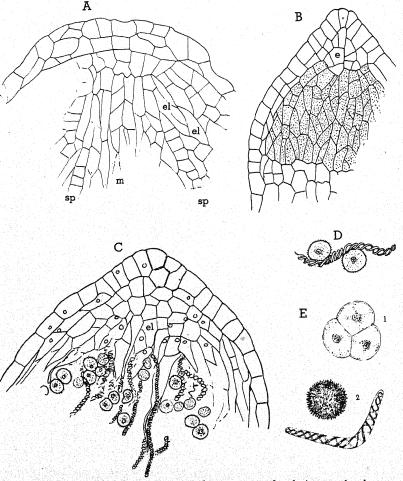


Fig. 67.-A, section of apical region of the young capsule of Aneura pinguis; sp, sporogenous cells; el, elaters; m, elaterophore; B, young capsule of Podomitrium; e, elaterophore; C, nearly ripe capsule, showing spores and elaters; D, ripe spores and elaters; E, Fossombronia longiseta; E, 1, young spore-tetrad; E, 2, ripe spore and elater (A, after Goebel).

irregular vertical rows. Some of the cells cease to divide from the young elaters; the others, by a series of cross walls, form the isodiametric spore mother cells, much as in *Dumortiera* or *Marchantia*. In *Pallavicinia* (*Blyttia*) radiculosa the sporogenous tissue in the young sporophyte is more extensive than in *P. Zollingeri*. In the former the capsule is much elongated

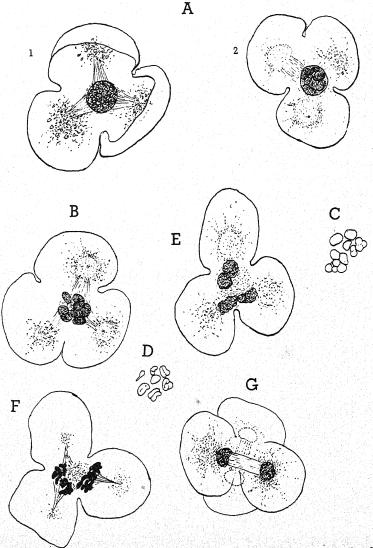


Fig. 68.—Spore division in Calycularia radiculosa. A, B, show quadripolar spindle; C, D, chromosome groups; G, successive bipolar division.

and has a conspicuous beak. Much like *Pallavicinia* in the structure of the sporophyte is *Podomitrium*. In *P. malaccense*, however, there is a small apical elaterophore which recalls that of *Aneura* but is much less developed.

Spore division.—Before the division of the nucleus the spore mother cell is conspicuously four-lobed, a character common to all the Junger-manniales but also found in *Targionia* and *Monoclea*. In *Pallavicinia decipiens* Farmer found that before the first nuclear division a "quadripolar" spindle was formed; after the reduction division was completed, the chromosomes at once divided without forming a nuclear membrane and the chromosomes formed four groups, which moved to the four poles of the spindle, where they developed the nuclei of the four spores.

In Calycularia radiculosa a similar condition may occur but sometimes there are two successive divisions with the formation of a bipolar spindle. In Calycularia the center of each lobe of the mother cell is occupied by a roundish body which perhaps marked the position of a centrosome, such as has been found in Pellia. In Pallavicinia radiculosa and P. Levieri there was no evidence of a quadripolar spindle, but in all cases seen there were two successive bipolar spindles.

After the four nuclei have assumed the resting condition, cell walls are formed simultaneously between them extending inward from between the lobes, completely dividing the mother cell into the tetrad of spores. Each spore develops about itself the thick wall which becomes differentiated into the thick protective outer wall and the inner cellulose membrane. The spores finally become entirely separated by the dissolution of the mucilaginous walls of the mother cell. With the ripening of the spores the elaters develop a double spiral band and the capsule wall may develop somewhat similar thickened bands (Calycularia, Pellia) or it may be uniformly thickened (Pallavicinia, Podomitrium).

CLASSIFICATION

The most recent attempt to classify the Anacrogynae is that of Goebel. Five families are recognized: Metzgeriaceae, Pelliaceae, Fossombroniaceae, Treubiaceae, and Calobryaceae. The Fossombroniaceae are most like the Sphaerocarpaceae and are probably the most primitive. The Calobryaceae differ so much from the other Jungermanniales that their separation as an order seems warranted.

FAMILY 1. FOSSOMBRONTACEAE

Fossombronia is, on the whole, the least-specialized number of the Anacrogynae and shows some significant resemblances to the Sphaerocarpales, especially Geothallus, from which it differs, however, in the structure of the sporophyte, which, like the other Jungermanniales, forms normal elaters and has the capsule wall composed of two cell layers.

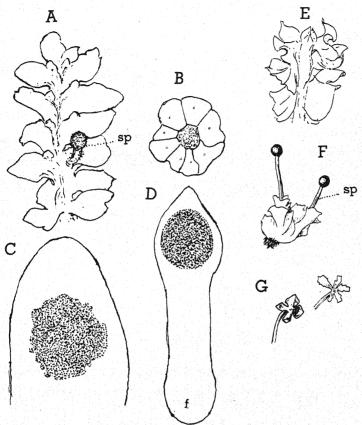


Fig. 69.—Fossombromiaceae, Treubiaceae. A-D, Treubia insignis; A, plant with young sporophyte; B, cross section of archegonium neck; C, apex of young sporogonium, showing extent of the archesporium; D, an older stage; f, foot; E-G, Fossombronia longiseta; E, thallus, showing leaf-like lateral lobes; F, plant bearing two sporogonia; C, two open capsules.

Fossombronia longiseta, a common California species, has a prostrate, sometimes dichotomously branched gametophyte, with a central thickened axis bearing on each side a row of somewhat irregularly lobed, leaf-like appendages. The leaves are composed of a single layer of cells but at the base merge somewhat gradually into the thickened midrib of the shoot. F. longiseta normally dries up completely in summer, reviving with the autumn rains. Sometimes, especially in southern California, subterranean tubers, like those of Geothallus, are developed. Goebel describes similar tubers in F. tuberosa.

The reproductive organs of Fossombronia are not segregated in definite receptacles but are scattered somewhat irregularly over the dorsal surface of the midr's near the base of the leaf. Unlike the condition in Sphaero-

carpales, there is here no involucre enclosing the young gametangia, but after fertilization a conspicuous bell-shaped perianth is developed about the archegonium. Under favorable conditions the development of young archegonia and antheridia continues for a long time. The archegonium sometimes has six rows of parietal neck cells instead of the five of the typical Jungermanniales.

As already indicated, the embryo of Fossombronia differs from that of the other Anacrogynae in the hypobasal origin of the foot, in which it resembles the Sphaerocarpales and Marchantiaceae. In F. Luetzebergiana

the elaters are imperfectly developed.

Probably related to Fossombronia is Petalophyllum Ralfsii which is said to resemble Geothallus in habit. It grows in sand near the sea, where it becomes partly buried and may form a tuber. There are two rows of well-defined leaves. The apical cell of Petalophyllum is tetrahedral, like that of the Acrogynae instead of like the two-sided form of most Anacrogynae. Goebel includes Petalophyllum and another genus, Sewardiella, in the Fossombroniaceae. Sewardiella also develops a subterranean tuber.

FAMILY 2. TREUBIACEAE

Treubia insignis, one of the largest and most interesting liverworts, was discovered in Java by Goebel. The same, or a closely related species, was later found in Patagonia, New Zealand, and Tahiti; and the writer collected a single specimen on Mt. Banajao in Luzon, Philippine Islands.

The thick, fleshy, prostrate stem has two rows of large, fleshy leaves, each leaf having a small scale at its base. The gametangia are in small groups at the base of the leaf and are protected by the scale. The plants are dioecious and sometimes the gametangia are replaced by multicellular gemmae. As in *Petalophyllum*, the apical cell is tetrahedral. It has been suggested by Goebel that the small basal scale of the leaf may be homologous with the "dorsal lobe" in *Gottschea*, an acrogenous genus which has other characteristics recalling *Treubia*.

While the position of the reproductive organs is much as in Fossom-bronia, the archegonium and sporophyte are here markedly different. A cross section of the neck of the older archegonium, especially near the base, may show as many as nine peripheral cells. The origin of the archesporial tissue is not nearly so evident and can be recognized only as a much later stage of development. The wall of the capsule has three to four cell layers and suggests the sporophyte of some of the Acrogynae. In the early stages of the embryo there is a conspicuous multicellular haustorium, whose relation to the early divisions of the embryo is not clear. There is a massive calyptra like that of Aneura or Pellia, but no perianth. The seta is long, and the ovoid capsule opens by four valves. These differences indicate that

the relationship with Fossombronia is at best a rather remote one and that Goebel's establishment of a separate family is justified. Goebel includes provisionally two other genera, Blasia and Cavicularia.

It seems probable that Fossombronia is quite independent of the other genera with which Cavers includes it in the family Codoniaceae. As Pellia is the best-known member of this family it may be desirable to adopt the name Pelliaceae, as Goebel has done.

FAMILY 3. PELLIACEAE

Goebel includes in his family Pelliaceae only two genera, Pellia and Androcryphia. The Codoniaceae, as interpreted by Cavers, includes Goebel's Fossombroniaceae and Treubiaceae, i.e., Fossombronia, Petalophyllum, and Treubia, as well as Blasia, Androcryphia, Calycularia, and Cavicularia. To these one might add Makinoa, which Cavers refers to his family Blyttiaceae.

Pellia is represented by three species widespread in the North Tem-

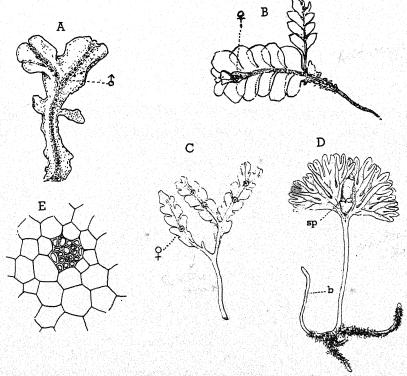


Fig. 70.—Pelliaceae, Metzgeriaceae. A, Pellia calycina; &, antheridia; B, Androcryphia confluens; &, archegonial receptacle; C, Symphyogyna sp.; &, female receptacle; D, Umbraculum flabellatum; sp., young sporogonium; E, section of conducting strand in Podomitrium.

perate Zone. The gametophyte is a simple thallus, the thicker median regions merging gradually into the thinner marginal region. The antheridia are scattered over the dorsal surface of the (male) plant, each sunk in a cavity. The archegonia are in a group near the apex of the thallus, situated in a pit whose margin forms an involucre about the receptacle. The archegonium has a very long neck, and the number of canal cells is much greater than in the other Anacrogynae.

The hypobasal cell of the young embryo takes no part in the further development of the sporophyte. The divisions of the young embryo are much like Fossombronia, and the origin of the archesporium is the same; but, as already stated, the foot as well as the other parts of the sporogonium are of epibasal origin. The foot is very conspicuous, and the seta becomes greatly elongated. The spores germinate within the capsule. The basal region of the archesporium is sterile and forms an "elaterophore," whose superficial cells develop into a tuft of fixed elaters occupying the bottom of the capsule. These elaters presumably assist in dispersing the spores.

Calycularia includes four species. The writer has studied C. radiculosa, a species of the Malayan regions but also reported from Samoa. It closely resembles Pellia in the structure of the thallus. Unlike Pellia, which is terrestrial in habit, Calycularia is epiphytic. It is dioecious, the males being smaller than the females. The antheridia are less numerous than in Pellia and are grouped in a sort of receptacle, each covered by a fringed scale. The antheridia in both position and structure are more like those of Mörkia than Pellia.

After fertilization there is formed a conspicuous bell-shaped "perianth" surrounding the archegonium. The structure of the sporogonium is much like *Pellia*, but no elaterophore is developed. *Calycularia radiculosa* differs in several important respects from the other members of the genus and shows some characters which indicate a nearer relationship with the Blyttiaceae. It might perhaps be made the type of a new genus, to some extent intermediate between Pelliaceae and Blyttiaceae.

Makinoa crispata is a monotypic species, according to Stephani, confined to Japan. The same, or a very similar species, was found by the writer in the mountains of northern Luzon, Philippine Islands. The plant closely resembles Pellia in the structure of the thallus and in the position of the archegonial receptacle. The antheridia are borne in a crescent-shaped receptacle instead of being scattered. The capsule is much like that of Calycularia, but the capsule wall is but two cells in thickness. The capsule opens by two valves as it does in Calycularia, but the valves may remain attached at the summit. The elaters have greatly attenuated ends, a character also shared with Calycularia. Hirata has shown that there is a definite elaterophore like that of the Aneuraceae.

Blasia pusilla, a monotypic genus, is widespread in the North Temperate Zone. Like Fossombronia the plant has a prostrate thickened axis which bears two rows of horizontal leaves. These are attached by a wide base, and the effect is a thallus with strongly lobed margins. On the lower surface near the base of each leaf is a small leaf-like organ suggesting the "amphigastria" of the acrogynous liverworts. There are also small hollow "auricles" which contain colonies of Nostoc, recalling the Nostoc infection of the Anthocerotes. The reproductive organs resemble those of Pellia; but the embryo is quite different and resembles in some ways the embryo of Frullania, one of the Acrogynae, and the elaterophore of Pellia is represented by only a few fixed elaters.

Blasia and the related Cavicularia densa from Japan are provisionally assigned to the Treubiaceae by Goebel.

Androcryphia (= Noteroclada) confluens is an interesting species, common in various parts of South America and also recorded from Mexico. It resembles Fossombronia but the leaves are more definite and in position resemble those of some Acrogynae like Lophozia. As in Treubia and Petalophyllum the apical cell is tetrahedral thus resembling also the Acrogynae.

Stephani recognizes only a single species, A. confluens. Schiffner states there are four or five species occurring in the Polynesian region and the Cape Verde Islands. A. confluens is monoecious and in general form and the distribution of the gametangia is much like Fossombronia. The numerous antheridia are scattered over the dorsal surface, and each is enclosed in a flask-shaped involucre closely resembling that in Sphaerocarpus. The archegonia are in the apical region, the leafy plant bearing them near the end of the shoot. The long-stalked globular capsule might readily be taken for a true acrogynous form.

Stephani considers *Pellia* as the nearest relative of *Androcryphia* and Goebel places them together in the family Pelliaceae. Like *Pellia* the spores begin to germinate within the capsule and there is a loose cluster of elaters at the base of the capsule recalling the basal elaterophore of *Pellia*. However, the general structure of the gametophyte and the arrangement of the reproductive organs suggest a closer relationship with the Fossombroniaceae.

FAMILY 4. METZGERIACEAE

The most specialized types of the Anacrogynae belong in the Metzgeriaceae. Goebel unites the two families of Cavers, viz., Aneuraceae and Blyttiaceae, into a single one, Metzgeriaceae, which he divides into three subfamilies: Aneuraceae, Pallaviciniae, and Mörkiaceae. Like Cavers he recognizes the difficulty of clearly defining these families.

ANEURACEAE

Goebel includes in the Aneuraceae four genera, Aneura, Metzgeria, Umbraculum, and Hymenophyton (Podomitrium). Aneura (= Riccardia) is much the largest genus and includes many species in the temperate and warmer parts of the world. The best-known species, A. pinguis, has a fleshy thallus resembling that of Anthoceros and is composed of practically uniform cells. In other species, e.g., A. multifida, the gametophyte is much branched. In A. lobata the prostrate thallus has a pinnate outline due to short lateral branches; but in other species, e.g., A. tamariscina, there are upright shoots having a central cylindrical axis, bearing much-divided lateral branches, so that the shoot closely resembles the pinnately divided frond of a small fern. These frond-like shoots arise from a prostrate rhizome. There are various other modifications found in other species. The apical cell in Aneura is two-sided, much as in Fossombronia. According to Stephani the apparent monopodial branching is the result of an unequal dichotomy, one of the branches being pushed to one side while the other continues the growth of the main axis.

The gametangia are borne on short lateral branches. In the male branch an antheridium is developed from each segment of the apical cell. Each antheridium occupies a separate chamber, and the two rows of antheridia correspond to the two series of segments cut off from the apical cell. The archegonia arise in the same way but they are limited in number and crowded together on the short receptacle. The neck of the archegonium is short, and in A. pinguis there are only four neck canal cells, as in Riccia and Sphaerocarpus.

In A. pinguis the hypobasal cell of the young embryo becomes greatly elongated and forms a haustorium, which penetrates deeply into the tissue of the gametophyte. As already stated, except for the haustorium, all the organs of the sporophyte are epibasal. The divisions are very regular, the embryo composed of several tiers of cells showing a regular quadrant division. The lowermost tier develops the foot, the intermediate ones the seta, and the apical ones the capsule, the first periclinal division in the latter separating amphithecium and endothecium. The originally uniform tissue of the archesporium becomes differentiated into the sterile cells of the elaterophore and the sporogenous tissue radiating from it, which later forms the spore mother cells and free elaters. The young sporophyte is surrounded by a massive calyptra, but no perianth is formed. The wall of the ovoid capsule is composed of two cell layers which show ring-shaped or thickened bars on their walls. The four valves of the open capsule bear at their tips the remains of the elaterophore with the tuft of attached elaters.

Metzgeria has also numerous species mostly confined to the tropics

and temperate regions of the Southern Hemisphere. They are mostly epiphytes, the delicate dichotomously branched thallus having a distinct midrib, while the rest of the thallus is composed of a single layer of cells. The gametangia are borne on short branches growing from the ventral surface of the midrib. The development of the sporophyte is like that of Aneura, but the elaterophore is somewhat less developed and the capsule is globular. Multicellular gemmae, developed within superficial cells of the thallus, have been described by Evans.

Whether Umbraculum and Podomitrium are more nearly related to the Aneuraceae or to the Blyttiaceae is difficult to determine. Umbraculum resembles a much-branched Metzgeria, and the position and structure of the gametangia are very similar. Podomitrium is much more like Pallavicinia in appearance; but the gametangia are borne on ventral branches. which, however, are much like sterile shoots often found in Pallavicinia. Podomitrium and Umbraculum have been placed in a common genus, Hymenophyton (Stephani); but the differences warrant the establishment of the separate genera. There are but four species, all except one, Podomitrium malaccense, which reaches Borneo and the Philippines, being confined to Australia, New Zealand, and Tasmania. In Podomitrium malaccense the thallus differs from that of the better-known P. phyllanthus in usually having one wing almost completely suppressed. The antheridial branches are short, flattened shoots attached to the ventral side of the midrib with the antheridia in two rows, each antheridium covered by a fringed scale, much as in Calycularia. The female receptacle is a very short branch, also ventral in origin. The group of archegonia is surrounded by an involucre with fringed margin; and later a conspicuous tubular perianth is formed, a feature absent in Aneura and Metzgeria but present in Calycularia. The early stages of the embryo, so far as known, are most like Pallavicinia. The young sporophyte is cylindrical, and the archesporium is clearly defined. The capsule wall has two layers in the earlier stages but later becomes three-layered, and at the apex becomes still thicker, forming a short beak. There are no spiral or annular thickenings on the parietal cells, and in these respects Podomitrium is like Pallavicinia. There is a definite apical elaterophore, which, however, is much less developed than in Aneura; and its fixed elaters are represented only by elongated cells without spiral thickenings. The sporophyte has a definite foot like Calycularia and the capsule splits into two valves. In P. phyllanthus the capsule dehisces by two to four slits, but the valves are coherent at the summit.

In both *Umbraculum* and *Podomitrium* the midrib is traversed by a strand of thick-walled, elongated cells, a condition characteristic of the Blyttiaceae but absent in the typical Aneuraceae.

BLYTTIACEAE (PALLAVICINIACEAE)

Cavers includes in the Blyttiaceae four genera, Mörkia, Blyttia (= Pallavicinia), Symphyogyna, and Makinoa. The last-named shows much more resemblance to Pellia in the structure of the gametophyte but the recent investigations of Hirata show that the capsule has an apical elaterophore and is more like Aneura. For this reason Goebel places it in the Aneuraceae. Mörkia, which Schiffner unites with Pallavicinia, is made the type of a special family, Mörkiaceae, by Goebel who also includes Calycularia. The Blyttiaceae differ mainly from the Metzgeriaceae in having the sexual organs on the dorsal surface of the ordinary shoots. Mörkia includes two species, both European, one of which, M. flotowiana, has been investigated by Cavers. Stephani includes Mörkia in the genus Calycularia. The prostrate thallus is much like Calycularia, but the midrib is more clearly defined. It is, however, less marked than in Pallavicinia and Symphyogyna.

Pallavicinia includes about forty species, mostly tropical in distribu-

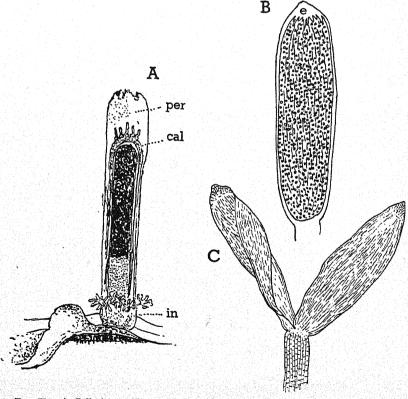


Fig. 71.—A, Pallavicinia (Blyttia) Levierii, sporogonium enclosed in perianth, per, and calyptra, cal; in, involucre; B, capsule of Podomitrium; e, elaterophore; C, open capsule of Podomitrium.

tion. Two sections of the genus are recognized by Stephani—Procumbentes and Dendroideae. These have also been considered as separate genera—Eupallavicinia and Mittenia (Gottsche). The first section includes those species with mostly simple prostrate thallus with very conspicuous thick midrib and broad, thin lateral wings, composed of a single cell layer. The midrib is traversed by a strand of elongated fibrous cells with thick, pitted walls. Branching is usually dichotomous, but adventitious lateral branches arising from the ventral side of the midrib are not uncommon.

In *Mittenia* there is a prostrate rhizome-like axis from which are developed erect, repeatedly dichotomous shoots, forming fan-shaped fronds much like those of *Umbraculum*. Along the margins are small teeth or spines. In both *Pallavicinia* and *Mittenia* the reproductive organs are borne on the unmodified thallus. The fan-shaped frond of *M. Zollingeri*, a species from Java and Sumatra, arises from the apex of the prostrate rhizome, which turns up and forks several times. Near the base of the upright shoot is an adventitious shoot which in turn gives rise to another frond. The secondary rhizomes apparently arise from dormant initial cells formed by a dichotomy of the apex of the rhizome.

The male plants are somewhat smaller than the females. The antheridia occur in elongated patches covering the central region of the frond. Each antheridium is covered by a scale like that of Mörkia or Calycularia.

Two East Indian species of Eupallavicinia, P. Levieri and P. radiculosa, were investigated by Miss Florence Williams. The latter-mentioned species is perhaps the largest member of the genus, the prostrate thallus being sometimes 20 cm. in length by 7 mm. in breadth. The midrib is very massive, the margin of the wings being entire. The male and the female plants are similar in size. The antheridia form a single row on either side of the midrib. The scales covering the antheridia are connected by a membrane which extends like a shelf along the side of the midrib. In P. Levieri the males are smaller than the females and a continuous membrane covers the row of antheridia. The development of the spermatozoids is much as in Calycularia; the chromosome number is eight.

The archegonial receptacle is surrounded by a cup-shaped involucre, and after fertilization the growth of the calyptra carries up the remains of the sterile archegonia. In *Mittenia* the calyptra does not involve the sterile archegonia.

The development of the archegonium in most cases follows the usual course; but in *P. radiculosa* the cap cell, instead of dividing at once into quadrants, may have several lateral divisions suggesting the segmentation of an apical cell adding to the growth of the neck, such as takes place in the mosses, and this has been reported in a number of Hepaticae by Gayet.

The archegonial receptacle is formed near the apex of the shoot but does not check its growth. The sporogenous tissue in the young sporophyte is more extensive in *Pallavicinia* than in *Mittenia* and more resembles *Podomitrium*.

The sporophytes differ a good deal in Pallavicinia and Mittenia. In the latter the oval capsule is about twice as long as wide. In Pallavicinia radiculosa it is almost cylindrical in form, and scarcely exceeding in width the short seta. The apex of the capsule has a conspicuous beak, which is wanting in Mittenia. The latter, also, has a well-marked foot, while in Pallavicinia the foot is almost indistinguishable. In both Mittenia and Pallavicinia the wall of the capsule, except at the summit, has an outer layer of large cells with uniformly thickened walls, within which are two or three layers of thin-walled cells. The capsule opens by four slits, the valves remaining coherent at the apex. The spores differ in the sculpturing of the outer wall. In Mittenia there are thick papillae somewhat like those of Calycularia, while in Eupallavicinia there is a network of fine ridges.

Symphyogyna.—In general appearance Symphyogyna so closely resembles Pallavicinia that the sterile plants are quite indistinguishable. About fifty species have been described, these being restricted to tropical America and the temperate regions of the Southern Hemisphere, especially Australia and New Zealand. Several species are found also in Hawaii. Some species closely resemble the "dendroid" type of Mittenia, while others are "Repentes," like Eupallavicinia. The latter often have the margin of the thallus toothed or lobed. The reproductive organs are much like those of Pallavicinia in structure and position, but the archegonial involucre is composed of a single scale like that of Podomitrium. The most marked difference is the complete absence of the perianth, which at once distinguishes it from either Pallavicinia or Podomitrium. The calyptra, however, is very conspicuous. Leitgeb has described the early stages of the embryo of S. rhizoloba, which are much like those of Pallavicinia radiculosa. The later stages of S. aspera show a similar correspondence. There is a limited apical growth which is also shared by Pallavicinia radiculosa.

The ripe capsule of Symphyogyna resembles that of Pallavicinia; the dehiscence is by four valves which remain united at the apex.

ACROGYNAE

The Sphaerocarpales, the Marchantiales, and the anacrogynous Jungermanniales are presumably ancient groups of which relatively few species have survived. The gametophyte is for the most part a prostrate thallus, growing on the ground or sometimes on rocks or logs. A smaller number, e.g., *Metzgeria* and *Calycularia*, are epiphytes. Some of the Anacrogynae show a marked tendency to develop leaf-like organs, which in such genera as *Treubia* and *Androcryphia* resemble closely the leaves of the "foliose" Jungermanniales, the Acrogynae. In both *Treubia* and *Androcryphia* the apical cell is tetrahedral like that of the Acrogynae, and it seems probable that from forms resembling these some of the Acrogynae have been derived. In both *Treubia* and *Androcryphia*, however, the archegonium is "anacrogynous."

While more than 7,000 species of Acrogynae have been described, more than seven times as many as all the other Hepaticae, their essential structure is very uniform. There is always a definite stem and leaves, the latter appearing most commonly in three rows, corresponding to the three series of segments of the tetrahedral apical cell. Like the Anacrogynae, the gametophyte is dorsi-ventral, and in a good many genera the ventral leaves (amphigastria) are not developed. A two-sided apical cell occurs in *Pleurozia* and *Arachniopsis* and in the early stages of *Metzgeriopsis*, but these are exceptional.

This stereotyped fundamental structure, and the great variety of minor variations within it, indicates that the Acrogynae are a highly specialized and presumably relatively modern group compared with the Anacrogynae. Except for the firm tissues composing the main axes of some of the larger species, e.g., *Bryopsis* and *Plagiochila*, both axes and leaves are composed of uniform parenchyma.

While the Acrogynae are cosmopolitan, some species even reaching the Arctic regions, they attain their maximum development in the rain-forests of the Tropics and the moist lowlands of the Southern Hemisphere. They may frequently be terrestrial in habit in the colder regions; but a larger number are epiphytes, especially in the tropical rain-forests, where they often cover thickly the branches of the trees and may form pendent masses of considerable size. Characteristic of the tropical rain-forest are the "epiphyllous" Acrogynae, especially many species of Lejeunea, often almost microscopic in size, covering the surface of the leaves of shrubs and ferns.

In the lower rain-forests of New Zealand some of the large terrestrial species of *Gottschea* and *Plagiochila* form extensive thick cushions on the forest floor. The excessive moisture of these forests promotes extreme vegetative growth and it is often difficult to find fertile specimens.

The epiphytic habit is probably a secondary development, and we may assume that the terrestrial habit, like that in most Anacrogynae, is the more primitive. Some of the terrestrial Acrogynae, like Nardia and Lophozia, resemble in general appearance the anacrogynous Petalophyllum or Androcryphia; and it is quite conceivable that from forms like the latter some of the more primitive Acrogynae have been derived. Cavers believes that the Acrogynae are derived from forms relating to Fossombronia; and

as Androcryphia is probably related to Fossombronia, it might be said to connect the Lophoziaceae with Fossombronia.

The gametophyte in Nardia bears numerous rhizoids on the ventral surface and two rows of dorsal leaves, composed of a single layer of cells. As in Fossombronia, the gametophyte is composed of uniform cells. In Lophozia the branching is dichotomous, as in the majority of the Anacrogynae. The archegonium, however, in Nardia and Lophozia is derived from the apex of the shoot, and they are definitely "acrogynous." In many of the Acrogynae the gametangia are borne on special branches, and they may be either monoecious or dioecious. While in such simple forms as Nardia the ventral leaves, or amphigastria, are often lacking, in many of the Acrogynae they are present. Frequently also the dorsal leaves are divided into two lobes.

Porella Bolanderi, a common and conspicuous species of coastal California, may be taken as a fairly typical representative of the more specialized Acrogynae. The genus is a fairly large one, comprising about 150 species, most of them tropical but with a number in the North Temperate Zone, including four in California.

P. Bolanderi grows upon shaded rocks or the base of tree trunks, and forms dense mats covering the substratum. It branches extensively, and the closely set overlapping dorsal leaves completely conceal the axis. On the ventral side is a central row of smaller leaves—amphigastria—and scattered rhizoids also grow from the ventral surface.

Each dorsal leaf in *Porella* is divided into a large (dorsal) and small (ventral) lobe, the latter bent under the larger lobe, and when seen from below, there seem to be two rows of small ventral leaves, in addition to the amphigastria.

A study of the apical growth in *Porella* illustrates the type common to most of the Acrogynae. The apical cell is a three-sided pyramid whose base (the outer free face) is an isosceles triangle, with the short side turned toward the ventral side of the shoot. From the apical cell three series of segments are cut off, two dorsal and one ventral. Each segment is first divided into an inner and an outer cell, and from the outer cell a leaf is developed. The two lobes of the dorsal leaves are determined by the first division in the mother cell of the leaf.

The branching in *Porella*—and this applies to most Acrogynae—is monopodial. A branch replaces the ventral lobe of a dorsal leaf. In the mother cell of the ventral lobe three intersecting walls cut out a pyramidal cell, which at once begins to function as the apical cell of the branch. This type of branching has been termed "terminal," and according to Evans, who has made an exhaustive study of branching in the Acrogynae, there are several variations of it. The *Frullania*-type represented by *Porella*

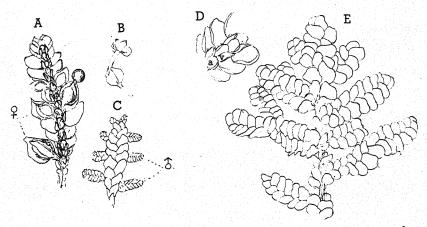


Fig. 72.—Porella Bolanderi. A, female plant; \mathcal{P} , archegonial branch; B, open capsule, showing four valves; C, male plant; \mathcal{C} , antheridial branches; D, lower surface of shoot; a, ventral leaves (amphigastria); v, ventral lobe of dorsal leaf; E, dorsal view of female plant.

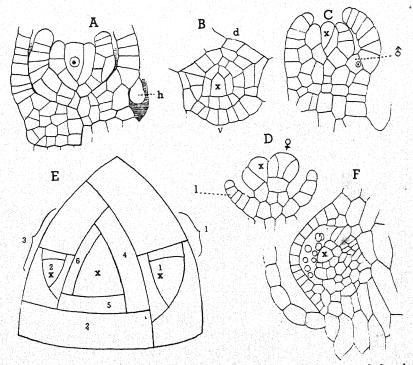


Fig. 73.—A, apex of shoot in Porella; B, cross section of apex; C, apex of male branch; \mathcal{C} , young antheridium; D, apex of female branch; \mathcal{D} , young archegonium; E, diagram, illustrating origin of branches in Acrogynae; F, endogenous branch in $Mastigobryum\ trilobata$ (E, F, after Leitgeb).

is the commonest. In most cases the whole of the ventral part of the segment, which ordinarily would produce the ventral lobe of the leaf, forms the bud; so that the leaf which subtends the young branch has only the dorsal lobe developed. In other cases only a part of the ventral lobe is devoted to forming the branch, and a rudimentary ventral lobe is present in the subtending leaf.

A second type of branching, termed intercalary, sometimes is found. These branches are for the most part endogenous in origin and usually arise from inner cells of the ventral segments of the apical cell. A typical example is the development of the "flagella" in *Bazzania*. The apical cell is covered by a single layer of superficial cells, which continue to grow and form a sheath about the growing bud. This finally breaks through and forms a slender shoot, "flagellum," bearing very much reduced leaves.

The leaves of the Acrogynae show much variation in form, but their development is very similar. They are usually closely set and partially overlapping. If the forward margin overlaps the base of the leaf above it is said to be "incubous"; if the forward margin is covered by the leaf above it, it is "succubous." In some cases, e.g., Lophocolea, the lobes are equal but more often, as in Porella, they are unequal. The margin may be entire, as in Porella, or variously toothed or much divided, as in Trichocolea. The amphigastria show a corresponding structure. In most cases the leaf is composed of a single layer of uniform cells. In a few cases, e.g., Gottschea, the leaves are several-layered (pluristratose) at the base, becoming thinner at the margin. In a few forms there is a midrib consisting of a band of elongated cells. Where the lobes are folded over, as in Porella, the lower one is smaller than the other; but less frequently the reverse is the case, as in Gottschea.

In many epiphytic species of the Lejeuniaceae, e.g., Frullania, the ventral leaf-lobe forms a sac, which apparently serves as a water reservoir. In the peculiar genus Pleurozia the water sacs are large, but the whole of the ventral lobe is not involved in their formation. In Pleurozia and some other forms these water sacs have a narrow opening which can be closed by a valve, which permits the entrance but not the egress of small animals like rotifers and other small aquatic organisms. These recall the vesicles in Utricularia, and it is thought they may serve the same purpose, the remains of the captured organisms serving to nourish the plant.

In the epiphytic species, as a rule, the rhizoids serve mainly for attachment, as the leaves absorb water quickly. Many species can be dried up indefinitely, reviving quickly when wet and at once becoming active.

Just as among the Anacrogynae there are forms like *Treubia* and *Noteroclada* which resemble the Acrogynae in habit and have the tetrahedral apical cell; thus there are several genera among the true Acrogynae

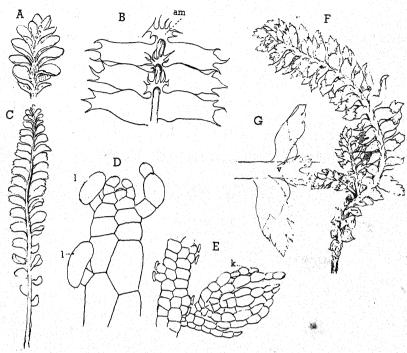


Fig. 74.—Types of Acrogynae. A, Lophozia sp.; B, Chiloscyphus combinatus; am, amphigastria; C, Plagiochila sp.; D, E, Zoöpsis; l, leaves; E, leafy bud, k; F, G, Gottschea; G, ventral surface; v, amphigastrium (B, after Schiffner; D, E, after Goebel).

which in their earlier stages have a thallose structure like that typical of the Anacrogynae. Goebel has made a special study of these and discovered one of the most remarkable forms, *Metzgeriopsis*, which at first forms a much-branched, flattened thallus, from which leafy shoots are later developed at the tips of the branches.

Two remarkable genera, Protocephalozia and Pteropsiella, were discovered by Spruce in South America. In the first there is developed a muchbranched, alga-like "protonema," recalling that of the true mosses. As in the latter, the leafy shoots bearing the gametangia arise as buds. These fertile shoots are typically acrogynous in structure. In Metzgeriopsis and Pteropsiella the early condition (protonema) resembles that in the Metzgeriaceae. In the first the thallus is composed of a single cell layer; but in Pteropsiella it is extraordinarily like that of Pallavicinia or Podomitrium. There are a conspicuous midrib and marginal wings. The branching is by ventral shoots developed from the midrib, and some of these ventral branches may develop into leafy, fertile shoots. The whole is remarkably like Podomitrium. Goebel considers the wings of the "thallus" to be equiva-

lent to a row of confluent leaves. While in *Metzgeriopsis* the apical cell is two-sided, in *Pteropsiella* it is tetrahedral and ultimately the apex of the "thallus" develops into a leafy shoot.

Another remarkable form, Schiffneria, is at first a flattened, thallose body with lateral lobes resembling the anacrogynous Blasia. The apex of the shoot finally develops into a short, leafy, fertile shoot with terminal archegonia. How far these peculiar Acrogynae are to be considered as connecting Acrogynae and Anacrogynae is a question. Goebel considers that they are reduced from typical Acrogynae. To the writer it seems there are valid reasons for assuming that they represent a condition intermediate between the two.

An extraordinarily reduced member of the Acrogynae is Zoöpsis, as small genus, one species, Z. argentea, being widely distributed in South America, Australasia, and the Malayan region. It is almost microscopic in size, the slender stem is composed of a small central axis of narrow cells surrounded by a single layer of large superficial ones. The leaves are reduced to mere rudiments—a pair of basal cells each bearing a small terminal cell. The fertile branches are formed on the ventral side, very much as in Pteropsiella, and these bear definite leaves. There are about ten species of Zoöpsis, all of which, except two West Indian species, are restricted to the Southern Hemisphere; and this is true of most of the other simpler and possibly primitive forms among the Jungermanniales.

Germination.—The germination of the spores has been described by a good many investigators. Hofmeister and Leitgeb studied various European species; and Goebel, Spruce, and others have examined a number of tropical forms which differ a good deal from the species studied by the earlier investigators.

One of the simplest cases is Lophocolea bidentata. There is first formed a short filament of four or five cells. In the terminal cell three intersecting walls establish the tetrahedral cell, which at once begins to function as the apical cell of the leafy shoot. The first leaves are simple cell rows, and none is developed on the ventral side; but by degrees the leaves assume the bilobed form of the adult gametophyte.

In *Trichocolea* Leitgeb states the development may be like that of *Lophocolea* but sometimes an irregular cell mass is formed before the definitive leafy shoot is developed.

In Frullania and Porella no filament is formed, and the early divisions result in an oval cell mass like that found in the ungerminated spores of Pellia. Just how the leafy shoot develops from this undifferentiated cell mass is still uncertain.

A quite different type is found in Radula. The germinating spore divides into equal quadrants, and further divisions result in a circular disc

composed of a single layer of cells, which later becomes two cells thick. A single large marginal cell divides to form the apical cell of the leafy shoot. The early leaves are rudimentary, but gradually the definitive form is developed.

The genus Lejeunea, which includes a large number of subgenera, is the largest genus of the Acrogynae. They are mostly epiphytic or epiphyllous and of small size. The young protonema in L. serpyllifolia has a definite two-sided apical cell like that of Aneura or Metzgeria. Metzgeriopsis, already referred to, has been referred to the same genus, i.e., Lejeunea Metzgeriopsis; but how far this condition is typical for the genus is at present uncertain. In L. serpyllifolia the two-sided apical cell is later replaced by the typical tetrahedral one found in the adult gametophyte.

Gemmae.—Simple unicellular or bicellular buds are found in many Acrogynae. These are most often formed from the margins or apices of leaves, and on being detached germinate very much as a spore does. Multical gemmae have also been described, especially in some of the tropical epiphytic species. In Cololejeunea Goebeli, an epiphyllous Javanese species, the gemmae are discoid plates attached to the leaf surface by a pedicel. This flat gemma has two growing points recalling the gemmae of Marchantia and Lunularia. When detached they become fastened to the leaf of the host plant by means of special mucilage-secreting cells.

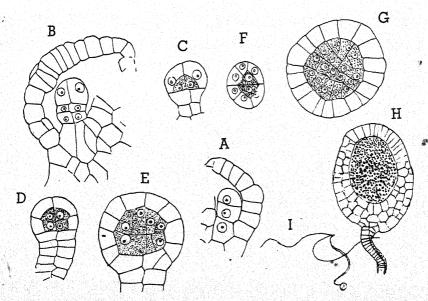


Fig. 75.—A-G, development of antheridium in Porella; H, ripe antheridium; I, free spermatozoid.

Gametangia.—The antheridia and archegonia of the Acrogynae do not differ essentially from those of the Anacrogynae. In the simpler forms like Lophozia and Nardia they are borne on the unmodified shoot; but in the more specialized types, like Porella, they are situated on special fertile branches. Both gametangia may be on the same individual, or the plants may be dioecious, the latter being the case in Porella, where the male branches project at right angles from the main axis. The closely imbricated, light-green leaves make them very conspicuous. In the axil of each dorsal leaf is a long-stalked antheridium. Sometimes, after the antheridia cease to form, the branch may continue its growth. The development of the antheridium corresponds in general with the usual type of the Jungermanniales but differs in having the basal portion of the capsule wall composed of two or three layers of cells. The elongated pedicel is composed of two cell rows.

The female branch is much less conspicuous. It originates in the same way as a vegetative branch, and the early divisions of its apical cell are the same; but only the first two or three segments develop leaves, after

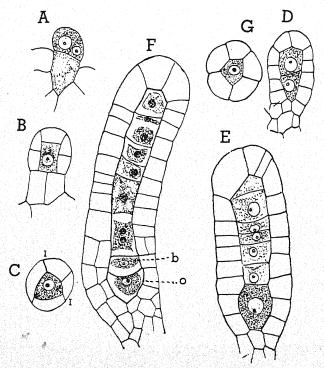


Fig. 76.—A-G, development of the archegonium in *Porella*; F, ripe archegonium; o, egg cell; b, ventral canal cell.

which each segment divides into an inner and an outer cell, the latter becoming at once the mother cell of an archegonium. The archegonia are then formed in acropetal succession; but finally a transverse wall is formed in the apical cell, which then develops into an archegonium, thus stopping any further elongation of the branch. The archegonium is typical, having five rows of peripheral neck cells and eight neck canal cells. Surrounding the group of archegonia is a "perianth," which after the fertilization of an archegonium becomes very conspicuous.

The archegonial receptacle in the Acrogynae is surrounded by an involucre or "perichaetium" composed of several more or less modified leaves. Within the perichaetium, in most cases, is a second envelope, the perianth, which recalls the perianth of such Anacrogynae as *Pallavicinia* or *Podomitrium*. The perianth of the Acrogynae, however, is sometimes considered to be formed by the fusion of the uppermost leaves of the shoot—two or three in number.

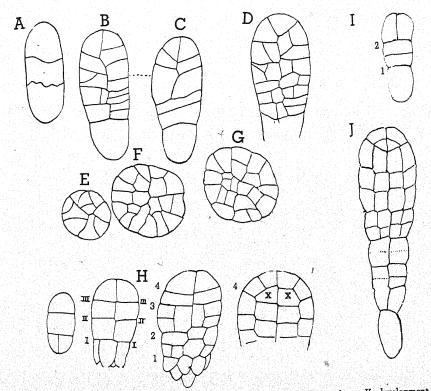


Fig. 77.—A-G, development of embryo in Porella; E, F, G, cross sections; H, development of embryo in Frullania; I, J, embryos of Radula (H-J, after Leitgeb).

Sporophyte.—The development of the sporophyte of the Acrogynae is known only in a very small number of forms, considering the immense number of described species. A few have been critically studied, but in most cases the results are very incomplete. It is evident from the forms that have been investigated that there are marked differences among them in the development of the embryo; and until a much more comprehensive comparative study of the embryology is made it will be impossible to establish a reliable classification of the Acrogynae.

While a majority of the genera examined agree in a general way, one large family, Lejeuneaceae, differs so markedly in the development of the sporophyte that Spruce considers them to be quite unrelated to the other Acrogynae and divides them into two "tribes"—"Jubuleae," comprising the Lejeuneaceae; and Jungermanneae, including all the other Acrogynae.

Frullania dilatata, a member of the Lejeuneaceae, has been thoroughly investigated by several investigators. Cavers gives a very full account of this species. The young embryo of Frullania consists of a row of three cells, as in most of the Jungermanniales. The hypobasal cell, however, instead of developing into a mere appendage or haustorium, as in most of the Anacrogynae, forms the foot, thus recalling Sphaerocarpus or Fossombronia. Each of the three primary cells is next divided into four equal quadrants, and the young embryo consists of three tiers of quadrant cells, much like Anthoceros. The terminal segment gives rise to the capsule, and the archesporium is established by the first periclinals as in Fossombronia or Aneura. The basal part of the capsule and the seta are developed from the middle segment. The hypobasal segment forms the foot, whose cells become elongated and presumably act as haustorial organs like those in the foot of Anthoceros.

The divisions in the four primary archesporial cells are extremely regular and for a time only vertical walls are formed, which results in a lens-shaped mass of elongated narrow cells. Some of these cells increase in width and by repeated transverse divisions become regular rows of spore mother cells. Alternating with these are the narrow undivided cells extending from top to bottom of the cavity of the capsule. These are the elaters, which become trumpet-shaped, with a single spiral band. The upper end remains attached to the capsule wall, which is composed of two layers of cells. The ripe capsule opens by four valves. "The valves spring outward with explosive violence, the spores being flicked away to a distance by the sling-like action of the elaters."

In Lejeunea serpyllifolia, belonging to the same family as Frullania, the hypobasal cell of the young embryo, according to Leitgeb, does not develop the foot; but the older stages seem to resemble Frullania.

¹ F. Cavers, Reprint from New Phytologist, No. 4, Cambridge, 1911, p. 120.

In Radula, of the three primary cells the hypobasal one forms simply an appendage, and practically the whole sporophyte is derived from the epibasal cells. There are several transverse divisions in the epibasal region before any vertical walls are formed; later, quadrant divisions are developed in the segments much as in Frullania, but the greater number of the segments results in a more elongated form of the embryo. In the terminal segment the first periclinals define the primary archesporial cells, but similar divisions in the segments below the apex also contribute to the archesporium, which is thus much more extensive than in Frullania but not so clearly delimited. Leitgeb states that the three upper segments contribute to the capsule. The arrangement of the archesporial cells is much less regular than in Frullania, although there is a tendency for the cells to be arranged in rows radiating from the base of the capsule; but no clear relation can be traced between the fertile and sterile cells.

Porella.—The early divisions in the embryo of Porella Bolanderi are less regular than those of Frullania or Radula. As in Radula, the hypobasal cell of the three-celled embryo undergoes no further development.

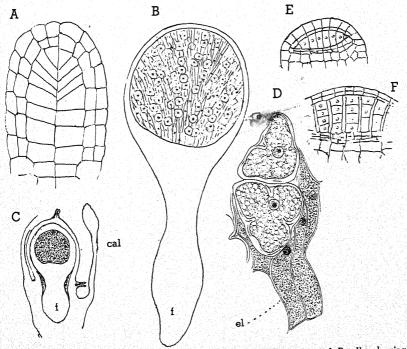


Fig. 78.—A, embryo of Jungermannia acuta; B, young sporogonium of Porella, showing spore mother cells and young elaters; f, foot; C, a similar sporogonium enclosed within the calyptra, cal; D, spore mother cells and young elaters, el, of Porella; E, F, young capsules of Frullania (A, after Leitgeb; E, F, after Cavers).

The early divisions in the epibasal region, while much as in *Radula*, are less regular and the succeeding divisions are more variable, so that the limits of the primary segments are less evident. The line between seta and capsule is very vague and the exact origin of the sporogenous tissue cannot definitely be made out. It is evident that the first periclinal divisions in the apical region do not determine the separation of the archesporium and the capsule wall.

The sporogenous region in the older stages shows more or less marked rows of cells radiating from the base of the capsule; but no definite relation between the spore mother cells and the elaters can be made out, the two being mingled without any apparent order. The spore mother cells, up to the time that the first indications of division are evident, are closely packed together with the young elaters. At this time the spore mother cells are somewhat angular in outline and deeply four-lobed. The cell wall is thick and striated, the inner layer of the wall becoming infolded and beginning to divide the cavity of the cell before the nucleus shows any evidence of division. With the further growth of the sporophyte the spore mother cells become isolated and the tetrad division is completed.

The seta is shorter than in many Hepaticae and merges somewhat gradually into the base of the capsule, whose wall is composed of two cell layers. The foot is less conspicuous than that in many other forms. Dehiscence of the capsule is by the typical four valves.

Cephalozia (Jungermannia) bicuspidata has been the subject of numerous investigations. The development most nearly resembles that of Radula. The hypobasal cell of the young embryo forms merely an appendage to the conspicuous foot, which like the rest of the sporophyte is epibasal. The embryo consists of a series of similar segments each divided into regular quadrants, and in addition to the apical quadrants several of the tiers below it contribute to the capsule. The limits of the endothecium (archesporium) are clearly marked off from the two-layered wall. The very long elaters are attached to the wall of the capsule and extend inward to the center of the capsule. When the latter opens, the elaters are thrown off, carrying with them the adherent spores. The wall of the capsule in the Acrogynae is commonly composed of two layers, but in some cases there are several.

Calyptra.—As the young sporophyte increases in size, the archegonium venter grows with it and usually forms a conspicuous calyptra, sometimes involving the tissues of the stem apex, and resembling the massive calyptra of some of the Anacrogynae, like Treubia and Symphyogyna.

Marsupium.—Sometimes the calyptra proper is rudimentary and the sporophyte is enclosed in a protective envelope developed from the outer tissues of the stem. This envelope is the "marsupium," evidently developed independently in several groups of the Acrogynae.

Among the more recent investigations on the structure of the marsupium, those of Goebel and Cavers may be cited. The latter has given an excellent résumé of the comparative morphology of the marsupium in the Acrogynae.

In the majority of the Acrogynae the young sporophyte is surrounded by three definite envelopes, viz., the calyptra, the perianth, and the involucre. All of these are quite free, and the foot of the sporophyte is included in the base of the calyptra. Sometimes, however, the perianth and the involucre may be more or less completely fused, or "concrescent," and the sporophyte completely invested by the calyptra is enclosed in a tubular sheath formed by the growth of a ring of meristematic tissue at the base of the involucre and the perianth, which carries up these structures to the top of the tubular marsupium (e.g., Gottschea).

In *Porella* the foot grows downward into the stem of the gametophyte and only the capsule remains within the calyptra, the seta and foot being enclosed in a short tube formed from the outer tissue of the stem. This is the simplest form of marsupium.

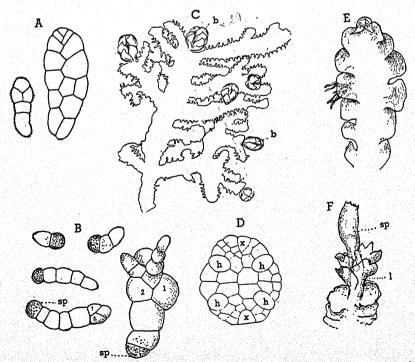


Fig. 79.—A, young plants of Lejeunea serpillifolia; B, germination of spores of Lophocolea bidentata; C, Lejeunea metzgeriopsis, protonema with leafy buds, b; D, gemma of Cololejeunea Goebelii; E, protonema of Schiffneria hyalina; F, S. viridis, developing the leafy shoot, bearing the sporogonium; l, leaves (A, C, D, E, F, after Goebel; B, after Leitgeb).

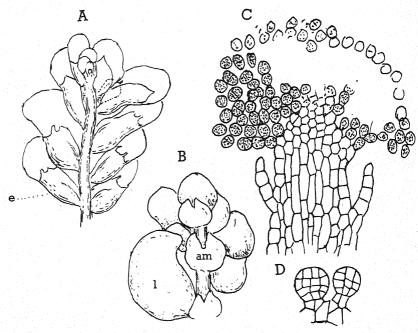


Fig. 80.—A, Cololejeunea Macounii; e, saccate ventral leaf lobes; B, Lejeunea sp. with saccate leaf lobes; C, Cephalozia bicuspidata, with unicellular gemmae; D, multicellular gemmae of Delayarella serrata (A, after Evans; C, after Cavers; D, after Goebel).

In some other genera, e.g., Gottschea, the venter of the archegonium is coherent with the apex of the stem, the young embryo is embedded in the tissue of the stem, and no calyptra is developed. The whole growth of the embryo is downward, so that the tubular sheath, the marsupium, is composed entirely of stem tissue.

In some prostrate genera, e.g., Calpogeia, Saccogyna, and Kantia, the marsupium develops on the ventral side of the shoot and penetrates into the earth, much like a true root. It is covered with rhizoids and no doubt provides for the enclosed sporophyte nourishment as well as protection.

The development begins as an enlargement of the tissue below the archegonium, and a cup-shaped depression is formed about the archegonial receptacle due to the active growth of the zone of tissue surrounding it. Growth is downward and the marsupium with the enclosed archegonia may reach a length of several centimeters. After fertilization the calyptra is formed, but the remains of the perianth and the involucre remain at the upper end of the marsupium.

A less specialized type of marsupium occurs in a few genera, e.g., Tylimanthus. Here the marsupium is solid and the embryo entirely embedded in it.

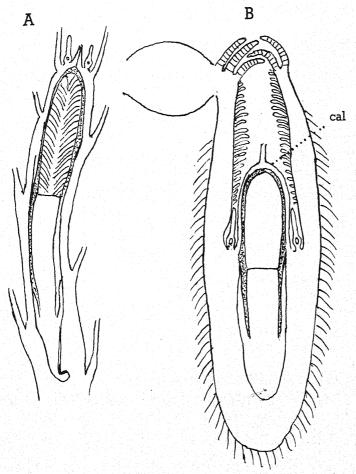


Fig. 81.—Marsupia. A, Gottschea; B, Kantia trichomanis (A, after Goebel; B, after Cavers).

CLASSIFICATION

The classification of the Acrogynae is in a very unsatisfactory condition. Cavers offers a somewhat tentative arrangement of the families but admits that it is to some extent an artificial one. His system is based in large part on that of Spruce. Eight families are recognized: (1) Lejeuneaceae; (2) Porellaceae; (3) Pleuroziaceae; (4) Radulaceae; (5) Scapaniaceae; (6) Ptilidiaceae; (7) Cephaloziaceae; and (8) Lophoziaceae. Cavers regards the Lophoziaceae as the most primitive family and the Lejeuneaceae the most specialized. The first four families may be considered as really natural ones. Of these the Lejeuneaceae differ so radically from the other

Acrogynae, in both gametophyte and sporophyte, that the family has been made a special section of the Acrogynae, a second section including the other seven famililes. The Lejeuneaceae is the largest family of the Acrogynae and has two thousand or more species, the greater number belonging to the old genus *Lejeunea*, which has been subdivided into some sixty or more subgenera. *Frullania* and *Jubula* are the other genera.

The family is largely tropical and mostly epiphytic, including many almost microscopic epiphyllous species. The leaves are typically bilobed, with the ventral lobe often saccate and forming a water sac. The peculiar sporophyte with the trumpet-shaped fixed elaters has already been referred to. Amphigastria are generally present.

The striking resemblance of the early stages of the gametophyte of some species to the Metzgeriaceae has been thought to indicate that the Lejeuniaceae may be descended from Anacrogynae of the Aneura or Metzgeriatype. The young gametophyte is a thallus with a two-sided apical cell which later is replaced by a three-sided one—from which later is developed the leafy shoot of the older gametophyte. Metzgeriopsis (= Thallo-Lejunea) is the most striking example. The Porellaceae include but a single genus, Porella, with about one hundred and fifty species. The greater number of species are tropical; but there are several species in the temperate regions, including four in California.

Pleurozia, sole genus of the Pleuroziaceae, has a single species in Europe, the rest being tropical. In Pleurozia the apical cell is two-sided, instead of the tetrahedral form of the other Acrogynae (except Arachniopsis). There are therefore only two rows of dorsal leaves developed, amphigastria being entirely wanting. The lower leaf-lobe is a hollow sac, having a valve at the opening, forming a sort of "trap-door" mechanism.

About two hundred species of *Radula*, the only genus of the family Radulaceae, are cosmopolitan, but only a small number occur in Europe and the United States. The dorsal leaves are divided into two lobes, of which the lower is much smaller and bears a tuft of rhizoids on its ventral surface. No amphigastria are developed.

These four families include only a minority of the Acrogynae. The great majority belong to the last four families, whose characters are difficult to define clearly. With the exception of the Scapaniaceae, in which the dorsal leaves are divided into lobes of unequal size, the leaves are either entire (e.g., Nardia) or the margin of the leaf is variously divided or toothed. Where they are deeply lobed, the lobes are equal in size.

The Scapaniaceae according to Schiffner include five genera, of which the most important are Scapania and Gottschea (= Schistochila). Gottschea includes some of the largest and most conspicuous of all the Hepaticae. It is restricted to the Tropics and the South Temperate regions.

G. appendiculata, abundant in New Zealand, is a very striking species. In size and general form it recalls Treubia, and Goebel has compared the small appendages at the base of the leaves in Treubia to the dorsal leaf lobes of Gottschea, which, like all the Scapaniaceae, are smaller than the ventral lobes. Gottschea has amphigastria, which are absent in some others of the family.

The Ptilidiaceae have the leaves usually much divided, sometimes the slender divisions branching. *Trichocolea* is notable for the repeated branching of the fine leaf divisions. Amphigastria are always present.

The family Cephaloziaceae includes about thirty genera, the majority tropical; but several, e.g., Cephalozia, Lepidozia, and Kantia, are cosmopolitan. The leaves are usually "incubous," the margin lobed or toothed; and amphigastria are generally present. Among the more remarkable members of the family are Protocephalozia and Pteropsiella, discovered by Spruce in South America, which develop a protonema comparable to that of Metzgeriopsis. The excessivly reduced Zoöpsis also is placed in the Cephaloziaceae.

The most primitive of the Acrogynae are probably the simpler forms belonging to the Lophoziaceae, like Lophozia and Nardia. It is these forms which seem to connect the more specialized Acrogynae with Anacrogynae of the Fossombronia type, e.g., Treubia, Petalophyllum, and Androcryphia.

The leaves are "succubous," or transversely inserted, closely resembling those of *Petalophyllum* or *Androcryphia*. They may be entire or two-lobed, and amphigastria may be entirely absent. The archegonia are borne at the apex of the main axis, which may be unbranched or branched dichotomously, recalling the predominant dichotomy in the lower Hepaticae. While many of the species are inconspicuous, *Plagiochila*, which is much the largest genus, has more than 750 species, some of which are among the most striking members of the Hepaticae.

INTERRELATIONSHIPS OF THE JUNGERMANNIALES

The comparatively small number of genera and species in the Anacrogynae and the very limited distribution of some of them, indicate that they are remnants of a more extensive ancient flora. As already noted, there is much difference of opinion as to their systematic arrangement.

Assuming that Sphaerocarpus is the nearest living representative of the ancestral forms of the existing Hepaticae, it seems probable that the living families of the Anacrogynae represent the remnants of several independent phyla. We may assume that the ancestors of the Hepaticae were thallose forms comparable to Sphaerocarpus, Aneura, or Pellia. Cavers divides the Anacrogynae into two primary groups, represented, respectively, by Pellia and Aneura. From the Pellia line he believes all of the Acrogynae have

been derived, Fossombronia connecting the lower acrogynous forms, like Lophozia, with the Anacrogynae. He does not accent Spruce's view that Lejeuneaceae have been derived from a Metzgeria-type, i.e., Cavers "Aneura" line.

There is in the Anacrogynae a marked tendency to develop leaf-like organs in some of them, e.g., Fossombronia and some related forms, closely resembling the leaves of Lophozia, Nardia, and others of the simpler Acrogynae. While Fossombronia thus suggests the simple Acrogynae, it also shows such marked resemblance to the Sphaerocarpales as to indicate its relationships are rather with the Sphaerocarpales than with Pellia. While Sphaerocarpus is ordinarily a simple thallus, it may under certain conditions of shade and moisture develop definite leaf-like lobes; and this is still more marked in Geothallus, which closely resembles Fossombronia in habit. There is also a good deal of similarity in the young sporophyte; and Goebel mentions a species, F. Luetzellurgiana, in which the elaters are imperfectly developed and the seta very short, thus approaching the condition in Geothallus.

There are several anacrogynous genera which approach the Acrogynae even more nearly than Fossombronia, to which they are probably related. These are Androcryphia, Petalophyllum, and Treubia. These in addition to their definite leaves also have the tetrahedral apical cell of the Acrogynae, instead of the two-sided cell of Fossombronia. Androcryphia and Petalophyllum may perhaps represent the end of a "Fossombronia" line, leading from the Sphaerocarpales directly to the Lophozia-type of the Acrogynae. Treubia, while showing some similarity to Fossombronia, differs much in its great size and the structure of the leaves, which also are very different from such Acrogynae as the Lophoziaceae. Treubia has some curious resemblances to Gottschea, one of the largest and most massive of the Jungermanniales. The family Scapaniaceae, to which Gottschea belongs, has leaves with two lobes, the upper one much smaller than the lower. The leaf in Treubia has a small appendage at its base whose nature is not certain, but this appendage has been compared by Goebel to the upper lobe of the leaf in Gottschea. Aside from the general similarity in size and texture of the two genera, there are certain features of the sporophyte which are suggestive. In Treubia there is a very large and massive calyptra, possibly comparable with the tubular marsupium of Gottschea. Assuming that Treubia is related to Fossombronia, it is conceivable that the Treubiaceae, branching off from the main line, may have developed a second phylum of Acrogynae represented by Gottschea.

The Metzgeriaceae of Goebel includes the three families, Aneuraceae, Pallaviciniaceae, and Moerkiaceae, thus uniting Cavers' two families, Aneuraceae and Blyttiaceae. They are strictly thallose forms, although in such types as *Umbraculum* and some species of *Pallavicinia* and *Aneura* there

may be a prostrate stem or "rhizome" from which arise the upright, much-divided shoots which superficially resemble the palmate or pinnate frond of a fern. A tendency to leaf formation is seen in some species of *Pallavicinia* and *Symphyogyna*, where the unistratose wings of the thallus are deeply lobed and might be regarded as leaves. In these species there is a definite strand of conducting tissue in the midrib.

In the Pelliaceae, Fossombroniaceae, and Blyttiaceae the gametangia are borne on the dorsal surface of ordinary shoots, as they are in *Sphaero-carpus*. In the Aneuraceae, as defined by Cavers, there are special fertile branches developed from the margin of the thallus, or from the ventral region of the midrib. This is presumably a secondary condition.

It is evident that the development of leaves, or leaf-like "fronds," has taken place independently in several families of the Anacrogynae. It is also apparent that this is the case regarding the presence or absence of a perianth.

The interrelationship of the Jungermanniales has been treated at length by Cavers, who makes clear that the line between the Anacrogynae and Acrogynae is not a definite one. There seems good reason to assume, as Spruce has done, that the Lejeuneaceae have been derived from types similar to the Aneuraceae. This is based on both the early development of the gametophyte from a thallose protonema with a two-sided apical cell and the development of the sporophyte, e.g., in Frullania, which is very similar to that of the Aneuraceae. Whether or not the "Jubuloideae" should be opposed to all the other Jungermanniales, as Spruce holds, is another question. The Lophoziaceae, as we have seen, have much in common with the foliose Fossombroniaceae. The gametophyte is simple in structure, with the gametangia borne on the unmodified shoot—where branching occurs it is mainly dichotomous, thus recalling the Anacrogynae. Cavers holds that from this simple type all the other Acrogynae have been developed and thus can all be traced back to the Fossombronia line.

The possibility of a third independent phylum is seen in the Cephaloziaceae. In the peculiar genus *Pteropsiella* the protonema is practically identical with that of *Podomitrium*, and the fertile branches (in this case leafy shoots) develop from the ventral region of the midrib exactly as in *Podomitrium*. The apex of the thallus also develops into a leafy shoot. Finally we have ventured to suggest the possibility of a connection between the isolated genus *Treubia* and *Gottschea*. This, of course, needs much more investigation. The weight of evidence would seem to indicate that the Acrogynae represent several independent phyla, derived from different anacrogynous groups, viz., Aneuraceae, Fossombroniaceae, and possibly Blyttiaceae (*Podocarpus*). As to the relationships among the Acrogynae as a whole, our knowledge of their ontogeny is too fragmentary to warrant anything but tentative conclusions.

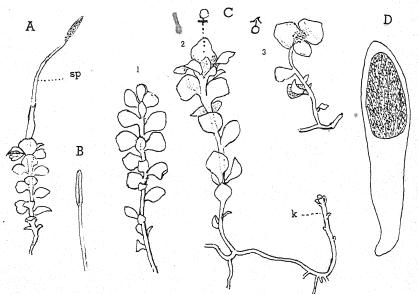


Fig. 82.—Calobryum Blumei. A, female plant with mature sporophyte; B, capsule showing dehiscence; C, I, plant with ventral leaves smaller; C, C, typical female plant connected with the "rhizome"; C, C, male plant; C, young sporogonium.

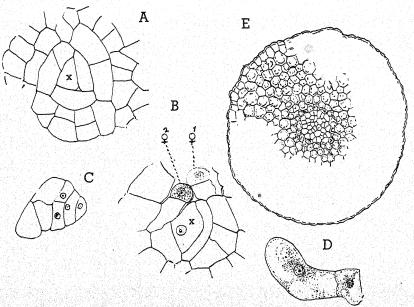


Fig. 83.—A, cross section of stem apex of Calobryum; B, apex of female plant with young archegonia; C, young leaf; D, hair; E, cross section of stem.

ORDER CALOBRYALES

The family Calobryaceae has been considered to belong to the Anacrogynae, but a study of the development of Calobryum blumei shows such great differences between this species and any of the other Jungermanniales that have been investigated that it seems desirable to remove the Calobryaceae from the Jungermanniales and to establish an order, Calobryales, co-ordinate with the other three orders of Hepaticae.

Of the six species representing the family, one, Haplomitrium Hookeri, occurs in several localities in Europe and has also been reported from one place in New Hampshire. The other five species of Calobryum are found in

the Malayan region, Japan, New Zealand, and tropical America.

The best-known species, C. Blumei, is found in Java and Sumatra. From the creeping rhizome, which branches freely, upright shoots develop, bearing three rows of distinct leaves, corresponding to the segments of the tetrahedral apical cell, the whole suggesting the leafy shoots of the acrogynous Jungermanniales. The leaves of one row are usually somewhat smaller

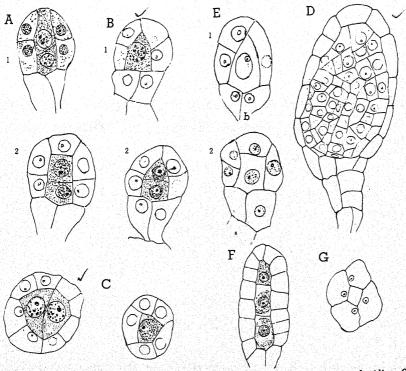


Fig. 84.—Gametangia of Calobryum. A, young archegonia; B, young antheridia; C, cross sections of young antheridia; D, older antheridium; E, F, young archegonia; G, cross section of archegonium neck.

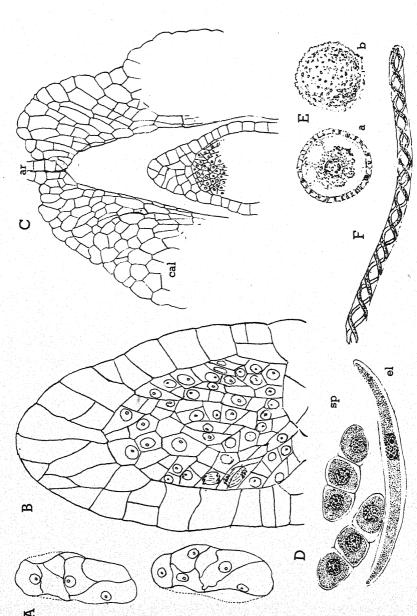


Fig. 85.—Calobryum. A, two sections of a young embryo; B, capsul of an older embryo; C, young sporogonium, with massive calyptra; ar, archegonium; cal, calyptra; D, sporogenous cells and young clater; sp, sporogenous cells; el, elater; E, ripe spores; a, section; b, surface view; F, elater.

and recall the ventral leaves or amphigastria of the leafy liverworts; but the general impression is of radial rather than of bilateral symmetry. The structures of the reproductive organs and sporophyte, however, differ essentially from any known member of the Acrogynae.

The rhizome is extensively branched but has no rhizoids. As in the dendroid Blyttiaceae, the leafy shoots arise from the ends of the rhizome branches. The roundish leaves are somewhat thickened at the base but are unistratose at the margin. A section of the stem shows a broad cortical region and a central cylinder composed of elongated cells, presumably for water conduction. The stem structure is like that in many true mosses, but so far as the writer is aware, is unknown in any of the acrogynous Jungermanniales.

Calobryum is dioecious, with the reproductive organs borne at the tip of the shoot, a whorl of three leaves surrounding the receptacle. The "inflorescence," especially in the male plant, recalls the male inflorescence in such mosses as Mnium or Funaria. In the female there are two or three

small leaves within the three large "perichaetial" leaves.

The early stages of the archegonium and antheridium are so much alike that for a time they are quite indistinguishable. While the divisions in the young antheridium may follow the type of the Jungermanniales, much more frequently the first division of the terminal cell is at one side of the median line and is intersected by two similar walls, as in a typical archegonium; and in cross section there are a central triangular cell and three peripheral ones. The mature antheridium is very much like that of many Jungermanniales.

The archegonia are formed from segments of the apical cell, and finally the latter is transformed into an archegonium. Calobryum is therefore

definitely "acrogynous."

As in the antheridium, there is a good deal of variation in the early divisions of the archegonium. In some cases no cover cell is formed, and instead of the five or six rows of peripheral neck cells there are only four. The neck canal cells are numerous, sometimes as many as sixteen to twenty.

The great similarity in the development of the archegonium and antheridium is of interest in connection with the question of the homologies of these organs. Goebel has maintained that they are really homologous, and his view is certainly strengthened by the conditions in Calobryum.

The young sporophyte resembles in form Pallavicinia or Podomitrium, there being no definite foot, and the apex forming a conspicuous beak. It differs essentially, however, in having the capsule wall composed of a single cell layer. In this it resembles the Sphaerocarpales and the Marchantiales. Of the latter, Monoclea most nearly resembles Calobryum in the elongated capsule and seta. The dehiscence of the capsule, by a single longitudinal cleft, is shared by *Monoclea*. There is no perianth developed in *Calobryum*; but, as in *Symphyogyna*, there is a conspicuous calyptra.

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CHAPTER VIII

MUSCI, TRUE MOSSES

The third class of bryophytes, the Musci or true mosses, greatly outnumber the Hepaticae in both species and individuals. With the exception of two small orders, Sphagnales and Andreaeales, they show an almost stereotyped structure and constitute one of the most clearly defined and highly specialized groups of plants.

Very little is known of their geological history; but from their evident adaptability to existing conditions it may be concluded that the predominant forms, the Bryales, are relatively modern types. While the Hepaticae are for the most part restricted to regions of moderate temperature and ample moisture, the mosses are ubiquitous, and especially in the northern regions may cover extensive tracts, almost to the exclusion of other vegetation. This is illustrated by the peat bogs of Northern America and Eurasia. In the forests of these regions, mosses often form a carpet over the forest floor and cover the fallen logs. Other species grow on the trunks and branches of trees. Some species of Sphagnum, Amblystegium, and Hypnum are aquatics. A good many mosses, e.g., Andreaea, grow on exposed rocks, often at high altitudes. Some species growing on decayed wood are, apparently, to some extent saprophytes. The most notable example is the genus Buxbaumia, where the leaves are rudimentary and the rhizoids penetrate the rotten wood very much as a fungus would do. Haberlandt mentions several other mosses, e.g., Webera nutans, which behave much like Buxbaumia.

The germinating spore in the mosses always gives rise to a distinct protonema, usually a much-branched, filamentous growth resembling a simple alga. The leafy shoot develops as a bud from the protonema. In Sphagnum and Tetraphis the protonema is a simple thallus, suggesting the gametophyte of some of the simpler Hepaticae or Anthocerotes. The adult gametophyte is always a leafy axis, recalling that of the Acrogynae; but there is little reason for assuming any relationship between the latter and the Musci.

The protonema may be permanent and the leafy shoot poorly developed in certain Phascaceae, but this is probably a secondary rather than a primitive condition. The growth of the leafy shoot is from a tetrahedral apical cell; the only known exception is *Fissidens*, which has a two-sided apical cell.

The protonema developed from the spore usually is transitory, but protonemal filaments may be formed from the rhizoids and may, like the primary protonema, produce leafy shoots. Secondary protonemata may, under certain conditions, develop from fragments of the leafy shoot, or even from the sporophyte. The larger mosses may also increase by the separation of branches. This is especially marked in *Sphagnum*, where this is the commonest form of reproduction.

Special buds or gemmae occur in a good many species, and are comparable to those found in the Hepaticae. These gemmae give rise to protonemal filaments from which leafy shoots develop, and may be composed of a few cells or may be multicellular, sometimes being borne in special receptacles, e.g., *Tetraphis*. Goebel has given an excellent account of these in his *Organographie*.

The gametophyte reaches in the Musci its most perfect development. Unlike the uniform tissues of the acrogynous Hepaticae, both leaf and stem of the higher mosses show a degree of differentiation comparable to

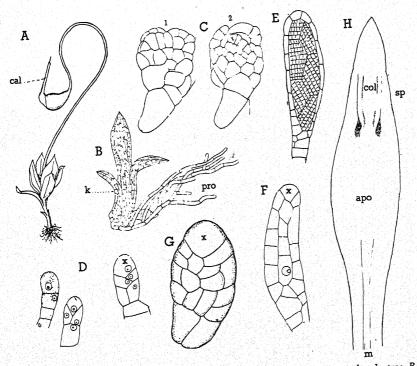


Fig. 86.—Funaria hygrometrica. A, leafy shoot with mature sporophyte; cal, calyptra; B, young leafy shoot, attached to protonema; C, young bud; C, I, outer view; C, 2, optical section; D, young, E, ripe, antheridia; F, young archegonium showing apical cell, x; G, young embryo; H, older sporophyte, sp, archesporium; apo, apophysis; m, central conducting tissue of seta.

the sporophyte of the vascular plants. The leaf has a definite conducting strand in the midrib, and the stem has an axial strand of conducting tissue, sometimes showing definite vessel-like elements very similar to the vascular elements in the ferns and seed plants. The outer portion of such stems forms a sort of "cortex" composed of thick-walled mechanical elements. The leafy axis in some of the larger mosses, e.g., Dawsonia, may reach a height of from 30 to 50 centimeters. So far as is known, the branching of the shoot is always monopodial.

The archegonia and antheridia of the Bryales both show a definite apical cell, in which respect they differ from the Hepaticae, although in some of the latter, a limited apical growth has been noted in the archegonium.

The sporophyte in the Bryales, which include most of the mosses, becomes highly specialized; but the early development is very uniform. Except in the Sphagnales the early growth of the sporogonium is always due to the activity of a two-sided apical cell. The establishment of the archesporium takes place at a late period and, like *Anthoceros*, it forms but a small part of the mass of the sporogonium. All the archesporial cells develop spores and no trace of elaters can be found.

The mature sporophyte (sporogonium) has the capsule borne on a conspicuous seta, but these are differentiated at a late stage, the young sporophyte being a greatly elongated cylindrical body with no indication of the limits of the capsular region. The latter finally grows rapidly in breadth and with its enlargement there is developed a very effective photosynthetic apparatus consisting of an extensive mass of green tissue with lacunae which may communicate with the outside atmosphere by means of stomata like those of Anthoceros.

√In most mosses the ripe capsule opens by a circular lid, the "operculum," with which are associated characteristic structures, the annulus and peristome. The former consists of several series of large, thin-walled cells at the base of the operculum. The peristome consists, in many mosses, of a circle of teeth surrounding the opening of the capsule (or "theca"). These teeth are hygroscopic and serve to dislodge the operculum, which is detached from the theca by the collapse of the cells of the "annulus" when the capsule is ripe. The structure of the peristome is of great importance in the classification of the many families and genera of the Bryales.

CLASSIFICATION OF MUSCI

Three orders of mosses may be recognized. Two of these, the Sphagnales and the Andreaeales, have but a single genus each. The great majority of the Musci may be assigned to a third order, Bryales, which, however, may be divided into four suborders. Two small families, Bux-

baumiaceae and Archidiaceae, might perhaps be considered as representing distinct orders, but they are probably to be looked upon as greatly modified members of the Bryales. This also applies to the much less aberrant "cleistocarpous" Phascaceae, whose development shows unmistakable relationship with the typical Bryales.

ORDER 1. SPHAGNALES

Generally recognized as the most primitive of the Musci, the Sphagnales are of special interest, as they show some striking points of resemblance to the *Anthocerotes* and may possibly connect these with the more highly developed mosses.

Sphagnum, the only genus, is cosmopolitan. There are numerous species in the northern parts of America and Eurasia, where they often cover extensive areas, especially the peat bogs characteristic of the northern regions but rare in the Arctic. They are essentially aquatic in habit, growing

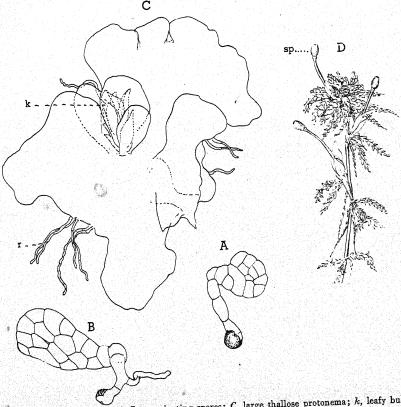


Fig. 87.—Sphagnum. A, B, germinating spores; C, large thallose protonema; k, leafy bud; r, septate rhizoids; D, S. squarrosom; sp, sporogonia.

about the margins of small lakes and ponds, or in depressions where water settles. In mountain regions they are often found growing on dripping, rocky banks. Species growing in the tropics are usually mountain forms; but sometimes, e.g., in Guiana and Trinidad, they may be found at sea level in boggy places in the savannas. There are a good many species also in the South Temperate Zone. Some of these aquatic peat mosses are long-lived and may reach a length of several feet, thus exceeding in length any other mosses.

The plants are extensively branched, and two types of branches may be present. At the apex of the shoot is a cluster of closely set short branches, while, at intervals below these, clusters of much elongated branches grow from the axis of the shoot. Some of these branches grow downward, forming a loosely interwoven mantle surrounding the axis of the shoot. Through this mantle water is drawn up by capillary attraction. The reproduction of the plant is largely vegetative, branches being detached and thus forming new individuals.

The leaves, instead of having the three-ranked arrangement of the acrogynous Hepaticae have a two-fifths divergence on the main axis. They have no midrib and there is no axial conducting strand in the stem, such as characterizes the higher mosses. Rhizoids occur in the young plant, but are almost completely lost in the older ones.

The germinating spore usually forms at first a short filament; this soon expands into a thallose protonema, which may have a definite two-sided apical cell like that in many thallose Hepaticae. This definite apical growth is soon lost, and the protonema becomes irregular in form. It is but one cell thick and is attached to the substratum by numerous rhizoids, which are septate. Similar septate filaments grow from the margin of the thallus and closely resemble the typical filamentous protonema of the Bryales. These marginal filaments may develop into secondary thallose protonemata.

The leafy shoot arises as a small bud near the base of the thallose protonema. There is soon developed a tetrahedral cell which becomes the apical cell of the young leafy shoot. The early leaves are composed of uniform cells, but the later leaves gradually develop the two sorts of cells found in the older plant.

The apex of the stem in the adult plant is a slender cone terminating in the tetrahedral apical cell, showing the regular succession of segments. The first division in the young segment is periclinal, the inner cell contributing to the axis of the shoot, the outer to the cortex and leaf. The leaf at first grows from a two-sided apical cell and the cells are alike. Later the apical growth ceases and the further growth of the leaf is basal. There then follows a differentiation of the cells of the leaf into two kinds—narrow green ones and large hyaline ones. The latter lose their chlorophyll and

become greatly enlarged, losing also their protoplasmic contents. These large cells show characteristic thickened bars upon their inner walls and the walls often have conspicuous round openings. A surface view of the leaf shows the large colorless cells enclosed in a network of the narrow green cells, which may be almost concealed by the bulging free walls of the swollen hyaline cells. The cortical cells sometimes closely resemble in appearance the hyaline leaf cells.

Gametangia.—Antheridia and archegonia are borne on slightly modified branches. The closely imbricated leavés of the male branches are often conspicuous, being red or yellow, and each leaf has in its axil an antheridium. The papillate mother cell divides by a series of transverse walls, forming a filament, the terminal cell finally developing the body of the antheridium. The cells of the pedicel undergo further divisions, so that it finally is composed of about four rows of cells. Sometimes there is a two-

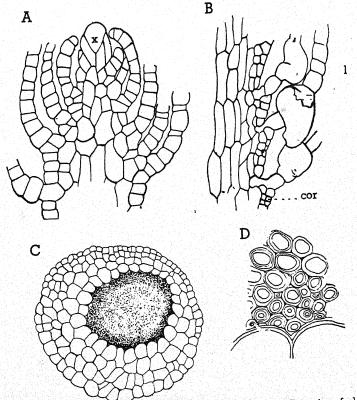


Fig. 88.—Sphagnum cymbifolium. A, shoot apex; x, apical cell; B, section of older part of stem; cor, cortical tissue; l, leaf-base; C, cross section of older stem; D, sclerenchyma from

central region.

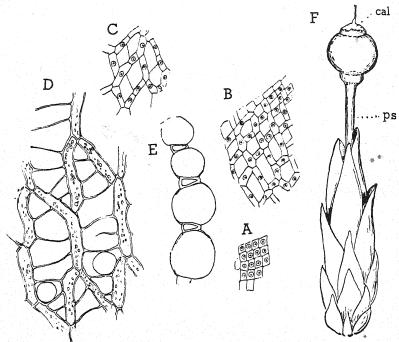


Fig. 89.—A-D, development of the leaf in Sphagnum cymbifolium; E, cross section of mature leaf; F, Sphagnum acutifolium, with mature sporogonium; ps, pseudopodium; cal, calyptra (F, after Schimper).

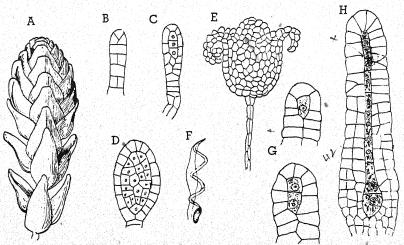


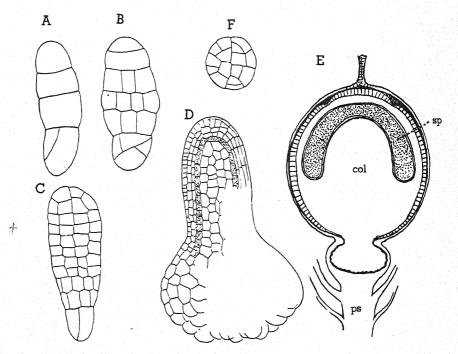
Fig. 90.—Gametangia of Sphagnum. A, male catkin of S. cymbifolium; B-E, development of antheridium in S. acutifolium and S. subsecundum; F, spermatozoid of S. acutifolium; G, young archegonia of S. subsecundum; H, mature archegonium (A, B, after Schimper; C, D, after Smith; G, H, after Bryan).

sided apical cell, like that in the Bryales, forming two series of segments; but according to Leitgeb there may be an imperfect third row of segments. Each segment is first divided by a radial wall into two equal cells, each of which is then separated into an inner and an outer cell. From the inner cells, by repeated division, the sperm cells are developed. The development of the spermatozoids resembles that of the Hepaticae. The spermatozoid is an elongated, spirally twisted body, with two long, slender cilia. The ripe antheridium has an oval form and in general appearance and position recalls that of *Porella*.

The structure of the archegonium is very much like that of the acrogynous Jungermanniales. The first archegonium is formed from the apical cell of the branch as in the Acrogynae, and secondary ones may develop from the last-formed lateral segments of the apical cell. The early development is exactly like that of the Hepaticae, the first divisions resulting in an axial cell and three peripheral ones. From the axial cell a cap cell is cut off, and the inner cell then divides into the central cell and the primary neck canal cell. The cap cell may undergo a definite quadrant division, as in the typical Hepaticae, or there may be a few secondary divisions, such as have been observed in a few Hepaticae. None of these divisions, however, contribute to the canal cells as is the case in the Bryales. The neck canal cells are usually eight or nine, and there are either five or six rows of peripheral neck cells.

Sporophyte.—In its earlier development the embryo also resembles the Jungermanniales, but the later stages are much like those of the Anthocerotes. The first wall is transverse; and the hypobasal cell, in which somewhat irregular divisions subsequently occur, suggests the hypobasal appendage of the Jungermanniales, while the organs of the sporophyte are derived mainly from the epibasal region.

The young embryo is composed of a row of about six cells. Each of the epibasal cells divides into equal quadrants and a periclinal division in each of these separates the amphithecium and the endothecium. At this stage the embryo resembles that of <u>Aneura</u>. Very soon the young sporophyte shows two regions, a terminal sporogenous one derived from the three upper segments of the young embryo, while the lower segments, together with the hypobasal one, enlarge rapidly and develop a large bulbous "foot," much like that of *Anthoceros*. There is, however, no meristematic zone between the foot and the capsule region. The origin of the sporogenous tissue (archesporium) is exactly the same as in *Anthoceros*, the archesporium being derived from the amphithecium by a periclinal division so that the endothecium, instead of developing the sporogenous tissue as it does in all the Hepaticae, remains as a sterile "columella" overarched by the layer of amphithecial archesporial tissue, exactly as in



* + Fig. 91.—A-D, development of the embryo of S. acutifolium; E, section of nearly mature sporophyte; sp, the spore sac; ps, pseudopodium; F, cross section of young embryo (all figures after Waldner).

Anthoceros. The archesporium is composed of four cell layers, thus resembling Notothylas or Megaceros rather than Anthoceros. Unlike both Hepaticae and Anthocerotes, all the sporogenous cells of Sphagnum produce spore tetrads.

The globular capsule is connected with the foot by a very short neck, no proper seta being formed, but as a substitute the axis of the shoot, which bears it, becomes much elongated and carries up the capsule beyond the perichaetial leaves. The apex of this "pseudopodium" is enlarged, owing to the growth of the sporophyte which is embedded in it.

The capsule has abundant chlorophyll, and a definite epidermis is differentiated, having rudimentary stomata like those in *Anthoceros* and the Bryales, but apparently never functional. The ripe capsule opens by a circular lid, or operculum. The beginning of this is indicated by a cessation in growth in a circular line of epidermal cells, forming a groove encircling the capsule and marking the margin of the operculum. The cells in this groove are thin-walled, and when the capsule is ripe these cells are ruptured and the operculum is thus separated from the capsule.

ORDER 2. ANDREAEALES

Like the Sphagnales, the Andreaeales have only a single genus. Andreaea contains almost a hundred widely distributed species. While there are some important structural resemblances with Sphagnum, in habit the species of Andreaea are very different. Instead of the aquatic habit of most species of Sphagnum the species of Andreaea, with few exceptions, grow in extremely exposed situations, especially on silicious rocks. They are found in the Arctic and Antarctic regions and in the Temperate regions of both hemispheres. In the tropics they are restricted to high mountains. They are small, dark-colored mosses, forming dense tufts, growing on granite or other silicious rocks.

The stem, like that of *Sphagnum*, has no axial conducting strand such as is usual in the Bryales. The leaves may have a simple midrib, but this is often absent.

The apical growth of the stem is much like that in *Sphagnum* and usually shows a similar three-sided apical cell; but the apical cell may be hemispherical, and segments are cut off from the base only.

Rhizoids of peculiar structure occur at the base of the shoot and, from these, buds develop which form new shoots. These rhizoids are cylindrical cell masses or flat cell plates, differing thus from the filamentous rhizoids of *Sphagnum*. The protonema, developed from the spores, is similar to the rhizoids, and the leafy shoots develop from them in the same way. There is thus no evident difference between the protonemal structures and the rhizoids. The thallose form of the protonema recalls that of *Sphagnum* and indicates a possible genetic relationship.

Gametangia.—Both the primary antheridium and archegonium are formed directly from the apical cell of the shoot, secondary ones being formed from the last-formed lateral segments of the apical cell. The young antheridium has a two-sided apical cell, like that in Sphagnum, a condition typical also of the Bryales. The early divisions of the archegonium are the same as in Sphagnum and the Hepaticae; but in Andreaea the cap cell, instead of dividing by quadrant walls, functions as an apical cell, from which four series of segments are cut off, the three lateral ones contributing to the peripheral cells of the archegonium neck and the basal segments forming the row of neck canal cells. The archegonium of Andreaea, therefore, has the same method of growth as that of the Bryales.

Sporophyte.—The first division in the embryo is transverse and divides it into nearly equal parts. The hypobasal cell divides somewhat irregularly, but in the epibasal cell two intersecting somewhat oblique walls form a two-sided apical cell. From this about a dozen alternating segments are formed, each of which is first divided by a median, radial wall so that a cross section of the embryo shows four equal quadrants.

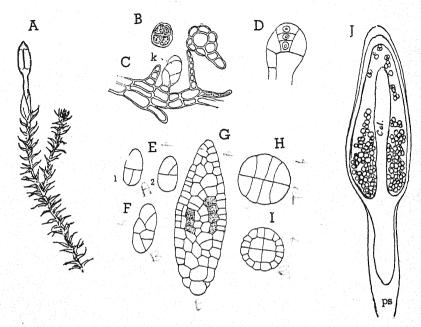


Fig. 92.—Andreaea petrophila. A, plant bearing ripe sporogonium; B, germinating spores and protonema; k, a leafy bud; D, young archegonium; E-I, embryogeny; I, section of ripe sporophyte (B-I, after Waldner).

In each quadrant a periclinal wall establishes the amphithecium and the endothecium, as in *Sphagnum*; but instead of the archesporium arising from the amphithecium, as in *Sphagnum* and *Anthoceros*, it is developed from the outermost cells of the endothecium as it is in the typical mosses, the Bryales. The archesporium is restricted to a small number of the segments in the middle region of the young sporophyte. Like *Sphagnum*, the archesporium extends over the summit of the columella. It becomes two-layered before the spore mother cells are differentiated.

As the capsule enlarges, a large lacuna is formed between the wall of the capsule and the columella. The ripe capsule opens by four longitudinal slits, somewhat like the dehiscence in *Pallavicinia*.

In both gametophyte and sporophyte, *Andreaea* is intermediate in structure between *Sphagnum* and the lower Bryales, and may perhaps be considered to connect the two orders Sphagnales and Bryales.

Archidium.—The species of Archidium are small mosses characterized by the small number but very large size of the spores borne in the globular sessile capsule. The early stages of the embryo resemble Andreaea, but the succeeding divisions are different. According to Leitgeb there is no definite archesporium and any cell of the endothecium is a potential

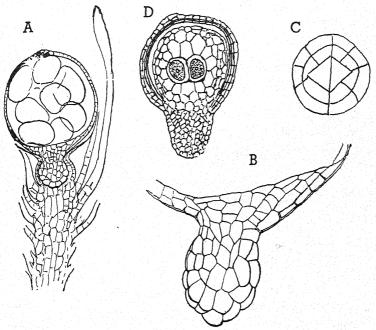


Fig. 93.—Archidium. A, A. Ravenelii, ripe sporogonium; B, foot and base of capsule; C, A. phascoides, cross section of embryo (diagram); D, sporophyte showing two large spore mother cells (C, after Goebel; D, after Leitgeb).

spore mother cell. The number of spore mother cells which develop rarely exceeds five or six. The sterile endothecial cells presumably serve to nourish the growing spores. No seta is formed, and the foot is embedded in the enlarged apex of the shoot. The capsule wall breaks irregularly, and in both the origin of the spores and the dehiscence of the capsule there is a suggestion of some of the simple Hepaticae.

Leitgeb regards Archidium as a primitive form allied on the one hand to Andreaea and on the other to some liverwort, possibly Notothylas. However, as the gametophyte and reproductive organs resemble those of the Bryales, it seems quite as likely that the view more commonly held—that Archidium is a greatly reduced form related to some group of Bryales—is correct. Cavers places it in the section Haplolepideae of the Eu-Bryales.

ORDER 3. BRYALES

All of the mosses except Sphagnum and Andreaea may be united into a single order, Bryales, which is separated into several groups, or suborders. Cavers recognizes four of these suborders, viz., Tetraphidales, Polytrichales, Buxbaumiales, and Eu-Bryales. This classification is based

mainly on the character of the peristome and the accompanying structures. Nevertheless in their essential features they are remarkably uniform; and although the details of both gametophyte and sporophyte offer great variety, the differences are not fundamental.

The number of species of the Bryales is very great, and they include the vast majority of the existing mosses. The greater number belong to the section Eu-Bryales, whose characteristics will be discussed before considering the other suborders.

In the Eu-Bryales the protonema is a filamentous alga-like structure, derived originally from the germinating spores but also formed secondarily from the rhizoids or, in exceptional cases, from the leafy stem or even from the fragments of the sporophyte. As a rule the primary protonema, i.e., that developed from the germinating spore, is short-lived and most of the leafy shoots are developed from protonemal filaments derived from the rhizoids. Multiplication by the detachment of branches of the leafy shoot is also common.

The rhizoids, which have thick cell walls and oblique septa, may develop chlorophyll and become transformed into green protonemal filaments, in which the septa are usually transverse. There is, in fact, no definite line between rhizoid and protonema. Both show a definite apical growth, a feature common to all the organs of the Bryales. The leafy shoots develop from buds, formed from either the rhizoids or the green protonemal filaments. The first stage is a papilla cut off from a protonemal cell. The papilla enlarges, and an oblique wall is formed near its base. This is followed by two similar oblique walls thus forming a terminal tetrahedral cell, which at once begins to function as the apical cell of the young shoot.

Very early in the development of the bud a rhizoid may form from one of the primary segments before any leaves are formed. No leaves are produced from the first segments and the first-formed ones are imperfectly developed. For some time the axis remains short and the leaves are crowded.

The apical growth of the older shoots is much as in Sphagnum. In each segment of the apical cell the first wall separates an inner from an outer cell. The latter then divides into an upper and lower cell—the former the mother cell of a leaf, the latter contributing to the cortical tissue of the stem or, in forms with branching habit, to the lateral shoots. The leaves grow from a two-sided apical cell and in the Eu-Bryales have a definite midrib. The rest of the leaf consists of a single layer of cells. The midrib may be composed of uniform cells, as in Ablystegium; but more commonly there is a strand of narrow conducting cells. A similar cylinder of conducting tissue occupies the center of the stem in most of

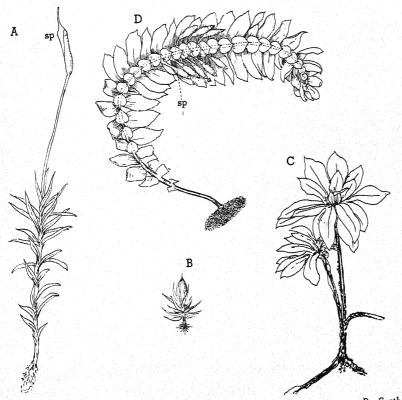


Fig. 94.—A, Catherinea augustata; B, Phascum sp.; C, Bryum giganteum; D, Cyatho-phorum pennatum; sp, sporophyte.

the Eu-Bryales. With the exception of Fissidens, which has a two-sided apical cell, the Bryales all possess the characteristic tetrahedral apical cell. In Fissidens the leaves are two-ranked, corresponding to the two series of segments of the apical cell. A condition strikingly like that of the foliose liverworts occurs in Cyathophorum, where there are two rows of dorsal leaves, and a ventral row resembling the amphigastria of the Acrogynae on the ventral side of the strongly dorsi-ventral shoot. This dorsi-ventral habit is seen in some other forms; but most of the mosses have the leaves placed spirally on the stem. The divergence is in nearly all cases more than one-third. In Funaria hygrometrica, a very common species, it is three-eighths.

The branching of the stem is with rare exceptions monopodial. The branch originates from the cortex, below a leaf. A cortical cell increases in size, and in it a tetrahedral cell is cut out very much as in the young

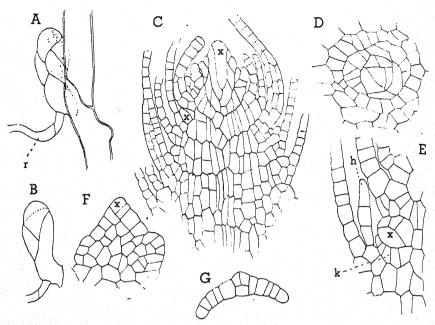


Fig. 95.—A, B, young bud developed upon a rhizoid of Funaria; C-G, Amblystegium riparium var. fluitans; C, stem-apex; x, young lateral bud; D, cross section of apex; E, young lateral branch, E; E, young leaf; E, section of leaf.

branch in the foliose liverworts. The tetrahedral cell becomes at once the apical cell of the young branch.

A section of the stem in most of the Bryales shows a central cylinder of narrow thin-walled cells, surrounded by a cortex, whose walls may be strongly thickened and dark-colored.

Gametangia.—The plants may be monoecious or dioecious. In the common Funaria hygrometrica, which is apparently dioecious, it has been shown that it really is "proterandrous," the male shoots developing first and the female shoot developing later as a bud from the base of the male. Where the plants are truly unisexual, as in Ceratodon purpureus, Marchal has shown that the spores also are unisexual and give rise, respectively, to male or female protonemata; and this is true of the secondary protonemal branches. In no case was the sex of the protonema influenced by external factors.

Antheridium.—In some mosses, e.g., Funaria, Mnium, and Polytrichum, the antheridia are formed at the apex of the shoot, the group of antheridia being surrounded by a circle of conspicuous leaves and the whole "inflorescence" looking much like an angiospermous flower.

The young antheridium very early develops a two-sided apical cell,

from which two ranks of segments are cut off in regular succession and the antheridium forms a cylindrical body borne on a short stalk. The early divisions in each pair of segments are very much like those in the young antheridium of the Jungermanniales. A cross section of such a pair of young segments shows two central triangular cells and a circle of peripheral ones. The formation of a periclinal wall in the apical cell finally stops its growth. The central cells divide rapidly into a mass of nearly cubical cells with little displacement of the primary segments.

The development of the spermatozoids is much like that of the Junger-manniales. Woodburn found six chromosomes in *Mnium affine* and *Polytrichum commune*. In the former the blepharoplast was evident in the androcyte after the final division. Allen found in *Polytrichum juniperinum* that they could be demonstrated during the last mitosis, and were identical with the central bodies (centrosomes) at the poles of the nuclear spindle. The originally globular blepharoplast becomes greatly elongated and fuses with the nucleus which forms the greater part of the slender coiled body

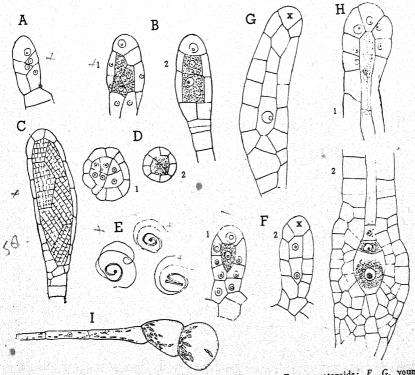


Fig. 96.—Funaria. A-D, development of antheridium; E, spermatozoids; F, G, young archegonia; x, apical cell; H, mature archegonium; I, paraphysis, from antheridial receptacle.

of the spermatozoid. The two long cilia are formed from the blepharoplast late in the development of the spermatozoid. Allen found a special body "limnosphere," in the androcyte, probably the same as the "nebenkörper," observed in various Jungermanniales.

The peripheral cells of the antheridium contain numerous chloroplasts, which sometimes, e.g., in *Funaria*, become bright orange-red in the ripe antheridium. The ripe sperm cells are discharged in a mass from the apex of the antheridium, and only gradually do they become completely separated and discharge the spermatozoids from the individual cells. Accompanying the antheridia there are often special hairs, "paraphyses." In *Funaria* these have conspicuous swollen terminal cells containing chloroplasts.

The early divisions of the archegonium are like those in Sphagnum and Andreaea; and as in the latter the cap cell assumes the character of an apical cell, from which four series of segments are cut off, those of the three lateral faces forming the outer neck cells while from the inner or basal face segments are cut off which form secondary canal cells. These may remain undivided or may undergo transverse divisions so as to increase considerably the number of neck canal cells. Each of the three lateral segments is first divided by a radial wall, and there are thus six rows of peripheral neck cells. The wall of the venter has two layers of cells.

In Mnium cuspidatum, Holferty found that at first the apical cell of the archegonium was two-sided like that of the antheridium, later being replaced by the typical three-sided one. This is the case also in M. undulatum, where Goebel found that there was a long period of growth in the stalk, with a two-sided apical cell before the archegonium itself was developed. In a number of mosses, e.g., Mnium cuspidatum, structures combining the characters of archegonium and antheridium have been found.

THE EMBRYO

Like the sex organs, the embryo of the Bryales shows a very definite apical growth. The first (basal) wall divides the embryo into nearly equal epibasal and hypobasal cells. The early divisions in both of these are much alike, oblique intersecting walls forming a two-sided apical cell, which, however, is not always present in the hypobasal region and in any case is soon lost. In the epibasal region the segmentation of the apical cell proceeds with almost mathematical precision.

Each segment first divides by radial wall into equal cells, and the next divisions separate the endothecium and the amphithecium, as in Andreaea.

The apical growth continues for a long time and the young sporophyte becomes a greatly elongated cylindrical body with no indication of a differentiation into capsule and seta. The endothecium forms a central massive cylinder surrounded by several layers of amphithecial tissue. Unlike Sphagnum, but resembling Andreaea, the archesporium is formed from the outermost layer of cells belonging to the endothecium. The cells lying immediately within the archesporium, forming the "inner spore sac," are sister cells of the archesporium.

The differentiation of the capsule begins at a late period and as the enlargement of the capsular region begins, there is the formation of air spaces or lacunae in the amphithecium. These begin to form between the innermost cell layer of the amphithecium (outer spore sac) and the much thicker outer portion. With the rapid growth of the capsule the lacunae become greatly enlarged, but some of the cells of the spore sac remain in contact with the outer amphithecial tissue and, with the expansion of the capsule, form filaments connecting the spore sac with the outer amphithecial

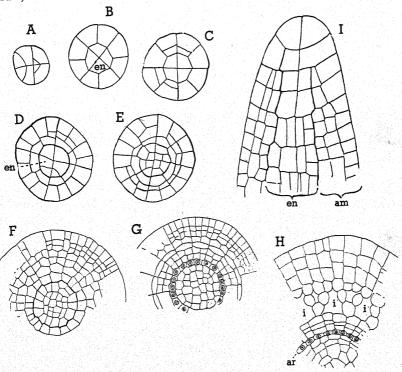


Fig. 97.—Funaria. A-E, series of cross sections of young sporophyte; F-H, similar sections from older stages; αr , archesporium; I, apex of young sporophyte, showing differentiation of amphithecium and endothecium.

cium. The archesporium is restricted to a limited region of the capsule and forms a cylinder occupying the median portion. The part of the endothecium lying within the cylinder of the sporogenous tissue is the "columella." The archesporial tissue does not extend above the columella but stops at the base of the operculum, which forms the upper part of the capsule.

Between the sporogenous region of the capsule and the seta there is a conspicuous enlargement, the "apophysis," merging gradually into the fertile part of the capsule. The apophysis is composed of chlorophyllous tissue and contains numerous lacunae. There is a well-marked epidermis with stomata much like those in *Anthoceros* or the vascular plants. The amphithecial tissue of the fertile region also has abundant chlorophyll,

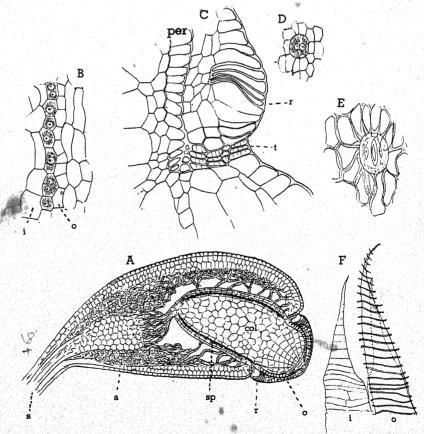


Fig. 98.—A, median section of full-grown capsule of Funaria; col, columella; sp, sporogenous region; r, annulus; o, operculum; B, the archesporium; o, outer, i, inner spore sac; C, junction of operculum and theca; to margin of theca, per, peristome; r, annulus; D, E, stomata, from apophysis; F, outer and inner peristome teeth.

and with the apophysis it forms a very efficient photosynthetic apparatus. Sometimes, e.g., in *Polytrichum* and *Splachnum*, the apophysis forms a well-defined appendage below the capsule. As the capsule enlarges, a furrow is formed around it some distance below the apex. This marks the limit between the sporogenous region ("theca") and the cap ("operculum") by which the opening of the ripe capsule is effected.

From the inner tissue of the operculum is derived a characteristic structure, the "peristome." In the majority of the Bryales it consists of a fringe of tapering membranaceous structures, the peristome teeth. In Funaria, for example, the peristome originates from the fifth layer of cells below the surface of the operculum. A section of the nearly ripe capsule shows these cells to have their outer cell walls strongly thickened, the thickening extending along part of the transverse walls. The inner walls are much thinner. The cells forming the margin of the theca are also much thickened and the peristome cells are attached to these.

Around the base of the operculum are several rows of cells, of which those first above the margin of the theca are large and thin-walled, while those above are thick-walled and compose the margin of the operculum. Before the final division of the sporogenous cells, the archesporium becomes more or less completely two-layered. All of the cells develop spore tetrads, and there is nothing corresponding to the elaters of the Hepaticae. The seta has a central strand of conducting tissue, much like that in the stem of the gametophyte; and the outer tissues are also thick-walled.

When the capsule is ripe, the foot of the sporophyte ceases to function and, the water supply being cut off, the delicate tissues of the columella and the inner parts of the operculum and the amphithecium collapse, leaving little except the spores, the epidermis of the theca and operculum, and the marginal cells of the theca with the attached peristome teeth. The rows of cells forming the peristome are split lengthwise, leaving two concentric rows of teeth corresponding to the outer and inner cell walls of the peristome cells. The large thin-walled annulus cells collapse, and the operculum is thus separated from the margin of the theca. The peristome teeth are highly hygroscopic and by their movements assist in throwing off the loosened operculum.

The young sporophyte remains for a long time enclosed in the calyptra, which becomes very large in the Bryales. It is finally torn away and carried up as a conspicuous cap covering the top of the sporogonium.

CLASSIFICATION OF BRYALES

With few exceptions the Bryales show extraordinary similarity in the structure of the sex organs and embryo, as well as in the origin of the sporogenous tissue, and the general structure of the mature sporogonium.

The classification of the many thousand species of the Bryales is still by no means settled. We shall adopt here—somewhat tentatively—the division of the order into four suborders proposed by Cavers in his excellent résumé of the mosses. He points out that the division of the mosses into two primary divisions, Cleistocarpi and Stegocarpi, still accepted by some systematists, is not valid. This division is based upon the method of dehiscence of the capsule, which in the Cleistocarpi is by irregular rupture of the capsule wall while in the Stegocarpi there is a definite operculum. Whether the Cleistocarpi represent primitive forms or are reduced from stegocarpous types is uncertain; it is evident that they do not represent a single natural assemblage but that some of them are evidently more nearly related to certain stegocarpous genera than to each other. The separation of the Stegocarpi into the divisions Acrocarpi and Pleurocarpi is also criticized by Cavers. This division is based on the position of the sporogonium. whether at the apex of the main shoot or on a lateral branch. Cavers points out that in certain "acrocarpous" families and genera, like the Leucobryaceae, Fissidens, Pleuroweisia, and others, pleurocarpous species are found.

He proposes as the main criterion of the classification the origin and structure of the peristome, a very constant character. On this basis he recognizes four main divisions (suborders) of the Bryales, viz., Tetraphidales, Polytrichales, Buxbaumiales, and Eu-Bryales.

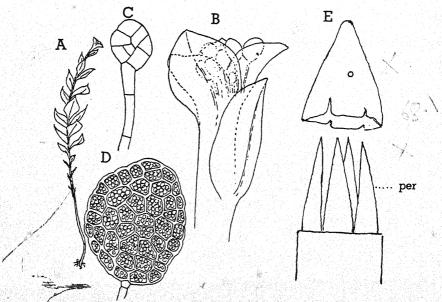


Fig. 99.—Tetraphis pellucida. A, plant with gemma cup; B, the same, more enlarged; C, young; D, mature gemmae; E, per, peristome, and, o, operculum (E, after Cavers).

SUBORDER 1. TETRAPHIDALES

The Tetraphidales include two small families, Calomniaceae and Tetraphidaceae, with less than a dozen species. The Calomniaceae are small epiphytic mosses, confined to the Southern Hemisphere. The three species of Calomnium occur in New Zealand and the South Sea Islands, growing on the stems of tree ferns. From a creeping main stem arise upright slender shoots bearing the long-stalked sporogonia. The leaves have a conspicuous midrib and the cylindrical capsule has a well-developed operculum, but no peristome is formed.

Tetraphis (Georgia) pellucida, a species occurring throughout the North Temperate Zone, represents the second family, Tetraphidaceae. Three other species of Tetraphis and one of Tetrodontium are restricted to the temperate regions of North America and Eurasia.

Tetraphis reproduces asexually by characteristic gemmae, which are borne in a terminal receptacle. This is a cup-shaped structure formed of a circle of leaves, the whole recalling the antheridial receptacles found in many mosses. The gemmae are formed in large numbers within the receptacle, and occasionally archegonia have been found within the same receptacle. The gemmae are borne on slender pedicels composed of a single row of cells, developing from the terminal cell of such a filament. The mother cell increases rapidly in size and becomes a discoid multicellular body which at first may show a definite two-sided apical cell, suggesting the early divisions of an antheridium. The gemmae become detached and from them protonemal filaments grow, from which leaf-like, expanded branches develop. These thallose branches recall the protonema of Sphagnum or Andreaea. The protonema developed from the germinating spores forms similar thallose structures. The leafy shoots arise near the base of these thallose protonemal appendages.

The structure of the leafy shoot in *Tetraphis* is like that of the other simple Bryales. The leaves have a definite midrib, and there is an axial strand of conducting tissue.

Tetrodontium brownianum is a small and probably reduced form growing in small caves and on the under side of noncalcareous rocks, especially in Central Europe. It has also been found in North America. The leaves are reduced in size and the short stem has no central conducting strand.

The capsule in *Tetraphis* is a cylindrical body, with a conspicuous conical operculum. When the operculum is removed, the peristome is seen to be composed of four solid pointed teeth. Sections of the younger capsule show no conspicuous lacunae between the sporogenous region and the amphithecium, and there are no stomata in the epidermis.

The origin of the peristome is very different from that of the Eu-Bryales. After the operculum is differentiated the whole of the tissue lying within it

splits into four equal parts, recalling the splitting of the elaterophore in *Aneura*. The four peristome teeth are thus composed of solid cellular tissue, unlike those of the Eu-Bryales, which are mere films of cell walls.

Tetradontium resembles Tetraphis in the structure of the capsule, but lacunae are present in the amphithecium and sometimes stomata are developed. Whether or not the peristome of the Eu-Bryales has been derived from a structure like that in Tetraphis is somewhat problematical.

SUBORDER 2. POLYTRICHALES

The very clearly defined suborder, Polytrichales, includes the most highly specialized members of the Musci. In *Polytrichum*, and especially *Dawsonia*, the gametophyte reaches the most complete development known among the embryophytes. The Polytrichales apparently represent a very distinct phylum, possibly most nearly related to the Tetraphidales but not connected with the Eu-Bryales. Except for about a dozen species of *Daw*-

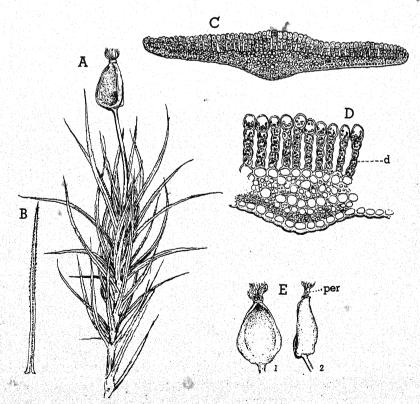


Fig. 100.—Dawsonia superba. A, plant with open capsule; B, a leaf; C, section of leaf; D, the same, more magnified; E, two views of the capsule; per, peristome.

sonia, representing the family Dawsoniaceae, all the other members of the Polytrichales may be assigned to the family Polytrichaceae. The Dawsoniaceae are characteristic of the Australian region, including New Zealand and New Guinea. One species has been reported from Borneo.

The most familiar of the ten genera belonging to the Polytrichaceae, viz., Polytrichum, Catharinea, and Pogonatum, which include the great majority of the approximately three hundred species, are cosmopolitan. Polytrichum commune, for example, is practically world-wide in its distribution. This well-known species has rigid upright shoots, sometimes 20 centimeters in length, with stiff, closely set, pointed leaves. The numerous rhizoids are often twisted together into cable-like strands. The leaves of

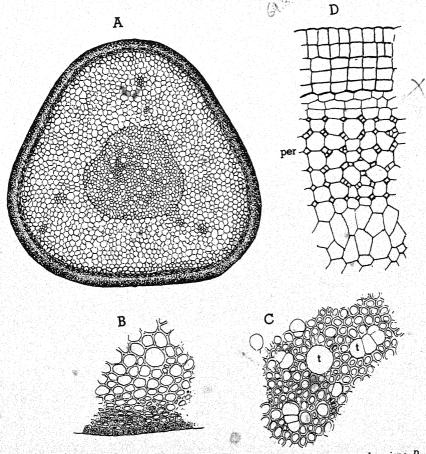


Fig. 101.—Dawsonia. A, cross section of stem; B, cortical region; C, central region; D, cross section of operculum; per, peristome (D, after Cavers).

Polytricaceae and Dawsoniaceae differ greatly in structure from those of other Bryales. A cross section of the leaf shows that except the extreme margin it is several cells thick and might be described as a greatly expanded midrib with a rudimentary lamina. This "midrib" shows a well-marked epidermis. Within the epidermis are closely set, narrow, fibrous elements between which are more or less definite rows of large thin-walled elements, suggesting the tracheary tissue of the vascular plants, and probably true water-conducting structures. From the upper surface of the leaf arise a series of parallel vertical lamellae composed of chlorophyll-bearing cells, and these green lamellae constitute the photosynthetic system of the Polytrichaceae.

The axis of the leafy shoot of the Polytrichales has a decidedly complex structure. Within the firm epidermis is a compact hypoderma of thickwalled, dark-colored elements. This merges somewhat gradually into the colorless ground tissue which composes the greater part of the axis. There is a conspicuous central cylinder composed of two tissue elements, narrow, dark-colored, sclerenchyma fibers and very much larger thin-walled cells almost destitute of protoplasmic contents and closely resembling the vessels of true vascular plants—doubtless true water-conducting organs. Traversing the ground tissue are slender strands of elongated cells—"leaf-traces"—structurally like the central cylinder but with the water-conducting cells less conspicuous. The leaf-traces finally unite with the central cylinder, in a manner quite like that found in the stems of many vascular plants.

The sexual organs of the Polytrichaceae agree closely with those of the Eu-Bryales. The male "inflorescence" is often very conspicuous, the leaves surrounding the antheridial group being broad and membranous in texture and reddish in color. The apex of the shoot may continue to grow after the antheridia have discharged the spermatozoids, the apical cell of the shoot not being directly involved in the formation of the antheridia, which are formed in groups at the base of the involucral leaves. Sometimes several antheridial receptacles are formed in succession on a shoot.

The Sporophyte.—The early stages of development of the embryo in Polytrichum are essentially as in Funaria and other Eu-Bryales. The apical cell, to judge from the recent study of P. juniperinum by Hildegarde Wenderoth, persists for a much longer time than in the Eu-Bryales. The early separation of the amphithecium and the endothecium is much as in the other mosses, but with the establishment of the archesporium and the details of the capsule and operculum Polytrichum differs much from the Eu-Bryales. After the segregation of the amphithecium, for a long time the further cell division is restricted to the amphithecium, and not until the latter has three to four layers of cells does division occur in the large primary cells of the endothecium. The first division, as in the Eu-Bryales,

separates the columella from the sporogenous region; but it is not until a later period that the actual archesporium is developed in the capsule, and the divisions in the endothecium are much less regular than they are in *Funaria* and other Eu-Bryales.

With the establishment of the archesporium the external differentiation proceeds rapidly. Instead of the cylindrical (or oval) form found in most mosses, in *Polytrichum* it is four-angled, and the apophysis is separated from the capsule by a marked constriction. As in the Eu-Bryales, with the expansion of the capsule large lacunae are formed; but these in *Polytrichum* occur in both the amphithecium and the endothecium. As in the Eu-Bryales, the archesporium is the outermost layer of the endothecium; but instead of its remaining only a single layer of cells it consists of several (four to six), according to Wenderoth, thus recalling the condition in *Sphagnum* and *Andreaea*.

The two inner layers of the amphithecium form the outer spore sac, as they do in *Funaria*; and between the spore sac and the next layer of the amphithecium the outer lacuna is formed, much as in *Funaria*. The second lacuna is formed between the inner spore sac and the columella. The stomata are restricted to the furrow separating the apophysis from the sporogenous portion of the capsule.

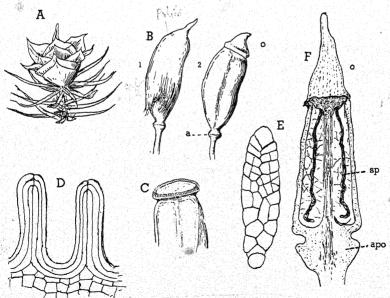


Fig. 102.—Polytrichaceae. A, antheridial receptacle of Catherinea; B, capsule of Polytrichum commune; B, I, covered with the calyptra; B, 2, calyptra removed; a, apophysis; e, operculum; C, open capsule of Polytrichum; D, peristome teeth; E, embryo of P. junipernum; F, section of a mature capsule of the same (D, after Cavers, E, F, after Wenderoth).

The development of the peristome is very different from that of the Eu-Bryales. The peristome is composed of bundles of thickened fibrous cells arranged in crescent form, the ends of the crescents pointing upward and joining the ends of the adjacent bundles. At maturity the peristome consists of a circle of 32 or 64 short pyramidal teeth surrounding the margin of the theca. The tips of the teeth are connected by a thin membrane "epiphragm," formed from the basal tissue of the operculum and stretched like the head of a drum over the opening of the capsule. Between the teeth are small openings in the margin of the epiphragm, through which the spores are discharged. The very large hairy calyptra completely encloses the capsule until it is full-grown.

Dawsoniaceae.—Dawsonia, the only genus of the family, represents the culmination of the gametophyte in the Musci. D. superba, the best-known species, is not uncommon in parts of southeast Australia and in New Zealand. The stout stems may reach a height of from 40 to 50 centimeters, and the narrow, crowded leaves are two or three centimeters in length. The anatomy of both stem and leaf is like that of Polytrichum but even better developed.

The structure of the sporophyte differs somewhat. Instead of the upright quadrilateral capsule of *Polytrichum*, the capsule in *Dawsonia* is dorsi-ventral in form, with the upper surface strongly flattened. The operculum is relatively much smaller than in *Polytrichum*. Instead of the short, thick peristome teeth of *Polytrichum*, in *Dawsonia* the peristome forms a dense tuft of much-elongated, slender teeth. A cross section of the operculum shows that these teeth form several concentric circles instead of a single one.

SUBORDER 3. BUXBAUMIALES

The family Buxbaumiaceae, with about half a dozen widely distributed species, represents the suborder. Here the gametophyte is greatly reduced, the leafy shoots being scarcely developed and the antheridia borne directly on the filamentous protonema. The protonema usually grows on rotten wood; the rhizoids penetrate into it and, according to Haberlandt, destroy it, behaving very much like fungus-hyphae; i.e., the gametophyte of Buxbaumia is partially saprophytic in its nutrition. This presumably accounts for the marked reduction in its structure.

Goebel considers the simple gametophyte in *Buxbaumia* as a primitive condition, and proposes to separate the Buxbaumiaceae from the other Musci as a distinct order. Cavers recognizes the Buxbaumiales as co-ordinate with the other main divisions of the Bryales.

The cells of the protonema contain chlorophyll, and on special branches are borne the globular long-stalked antheridia, each subtended by a color-

less scale. The archegonia, one or two in number, are formed at the apex of greatly reduced leaf shoots, the leaves having little chlorophyll and no midrib. From the bases of these shoots are formed the numerous colorless rhizoids which penetrate the substratum and thus supply the shoot, and subsequently the developing sporophyte, with nutriment. After fertilization there is formed a thick sheath about the foot of the sporophyte which is nourished through the activity of the rhizoids until it develops chlorophyll in the capsule, which is large, and has the same general structure as that of the other Bryales.

The sporophyte has a marked superficial resemblance to that of Dawsonia. It is strongly dorsi-ventral, with flattened dorsal surface and protuberant ventral region. The small operculum and the origin of the peristome also resemble Dawsonia. As in the latter, the peristome is formed from several concentric cell layers of the amphithecium; but there is a

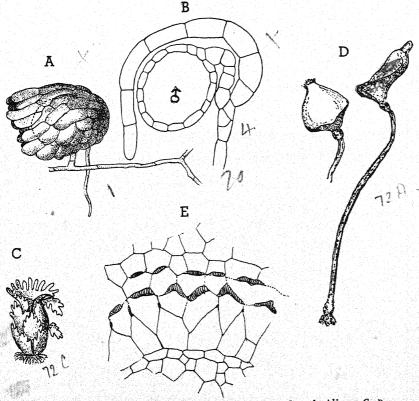


Fig. 103.—Buxbaumia. A, B, male plants of B. indusiata; &, antheridium; C, B. aphylla; D, Buxbaumia sp., showing mature sporogonia; E, cross section of the peristome of B. aphylla (A, B, E, after Goebel; C, after Rhuland).

differentiation into an outer and inner peristome, the outer composed of one to four series of slender teeth, and the inner (endostome) a thin tubular membrane having sixteen or thirty-two longitudinal folds. According to Goebel the outer peristome is lacking in B. aphylla, but in B. indusiata there is also the outer peristome. Both inner and outer peristome consist of cell membranes only, as in the Eu-Bryales, and not of entire cells, thus differing from the Polytrichales and Tetraphis.

The very marked resemblances between the sporophytes of Buxbaumia and Dawsonia suggest a real relationship, in spite of the fact that the latter has the most highly developed gametophyte of all the Musci while in Buxbaumia it is the most reduced.

Perhaps related to Buxbaumia is the cosmopolitan genus Webera, with about a dozen species, representing the family Weberaceae. As in Buxbaumia there is evidence here that the protonema is to some extent saprophytic, and there are formed upon it expanded green organs suggesting the thallose branches found in Tetraphis. The leafy shoots are short, without any central conducting strand. The leaves, however, have a conspicuous midrib which in some species is very broad and recalls the leaf-structure of the Polytrichaceae; but the cells are all alike and there are no traces of the vertical green laminae of the Polytrichales. The peristome is double, the outer consisting of a circle of sixteen short teeth, recalling the peristome teeth of Polytrichum; the inner peristome is like that of Buxbaumia—a conical membranaceous structure with sixteen vertical folds.

SUBORDER 4. EU-BRYALES

Owing to the enormous number of species in the Eu-Bryales it will be quite impossible to deal with the details of structure and the relationships of the hundreds of genera included in the order. Only a very small number have been critically investigated; and the classification, for the present, is largely based on somewhat superficial data. Much more extensive comparative study of the development is needed, especially of the capsule and peristome, before a definitive arrangement of the families and species can be attained.

The Eu-Bryales include the vast majority of the existing mosses which occur under almost every condition of life, except in salt water. Most of them can endure long periods of drought, reviving quickly when water is supplied. Usually there is a very definite stem, with the leaves placed spirally, and for the most part the stem has a well-marked central cylinder of conducting tissue and the leaf has a lamina composed of a single cell layer and a definite midrib. The leaves, of course, show many modifications, connected with the environment. In the majority the leaves are placed equally about the axis; but some genera are markedly dorsi-ventral in form, and in *Fissidens*, corresponding to the two-sided apical cell, the leaves are

in two rows. This is also the case in Bryoziphion. In Cyathophorum there are two rows of large dorsal leaves and a ventral row of small ones, so that the plant looks very much like a large foliose liverwort. In Schistostega there is a two-ranked arrangement of the leaves; but the leaves are placed vertically and the bases are united, so that the shoot has the appearance of a pinnate leaf. These are but a few of the many arrangements found in the leaves of the Eu-Bryales. The one-third divergence seen in Cyathophorum occurs also in Fontinalis and a few others; but in most cases there is a larger divergence, e.g., in Funaria it is three-eighths.

Branching in the Eu-Bryales is never dichotomous. In many cases the shoots are unbranched, but often there is extensive branching and the plants reach considerable dimensions. Sometimes there is a conspicuous rhizome from which aerial shoots are produced, e.g., Climacium.

CLASSIFICATION OF THE EU-BRYALES

The most recent complete account of all the families and genera of the Bryales is by B. F. Brotherus.¹

Cavers in his review of the Musci gives an excellent summary of the classification of the Eu-Bryales, which he defines as follows: "The peristome-forming zone consists of either two or three layers of cells, the walls of which become thickened in such a way as to form flat triangular teeth, the unthickened walls becoming resorbed so that the teeth consist of plates representing the thickened portions of the walls of either two or three concentric cell-layers. The horizontal walls in some cases do not undergo complete resorption, so that the teeth are then chambered and appear in longitudinal section to consist of a row of cells; though these cells are open on either side of the tooth. The number of teeth is typically either sixteen or thirty-two, more rarely eight or sixty-four. Where resorption is incomplete (e.g. Splachnum, Splachnobryum, Leptostovum, Leucodon) the peristome is regarded as being in reality double, and it is an open question whether the 'chambered' type of peristome is primitive or reduced. The Eu-Bryales are divided, in peristome structure, into three series."

In the first group, Haplolepideae, there is a single series of peristome teeth composed of membranes derived from two concentric cell layers. The sixteen teeth either are single or are more or less completely divided into two or three lobes or filaments. In some of them there is a collar-like "properistome" outside the peristome. Cavers recognizes five sections of the Haplolepideae. The first, Archidioideae, with the single, very much-reduced genus Archidium, is questionably placed in the Bryales; the systematic position of Archidium has already been referred to in the preceding

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¹ Engler and Prantl, *Die Natürlichen Pflanzenfamilien*, 2d ed., Vols. 10, 11, 1924-1925.

chapter. The second section, Dicranoideae, have the teeth usually cleft and include some well-known genera—Dicranium Fissidens and Leucobryum. The other sections, Monocranoideae, Ditrichocranoideae, and Platycranoideae, include about a dozen families. The second series, Heterolepideae, includes but a single small family, Encalyptaceae. This family is characterized by the great development of the calyptra, which continues to grow for a very long period and becomes detached only when the operculum falls off. While in Encalypta there is great uniformity in all other characters, the peristome varies greatly. "It may be constructed either on the Haplo-lepidean or the Diplolepidean plan, and in the latter case the superposed exostome and endostome are sometimes coherent, owing to incomplete resorption of the horizontal walls of the peristome-forming cells." It has been suggested that Encalypta represents a synthetic ancestral type from which the two series, Haplolepideae and Diplolepideae, have been derived; but this does not seem very probable.

The Diplolepideae include the major part of the Eu-Bryales; and in these, with few exceptions, the peristome is double, although there are genera (e.g., Splachnum) in which it is apparently single and a few others (Gymnostomium) where no peristome is present. The outer peristome

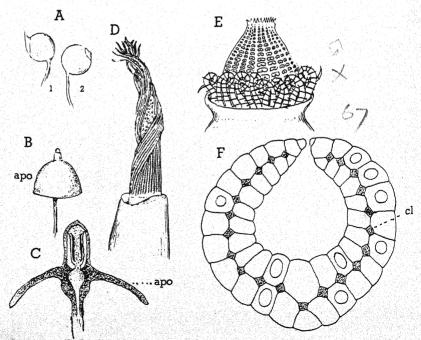


Fig. 104.—Eu-Bryales. A, Bartramia sp.; B, Splachnum, sp.; apo, the apophysis; C, section of B; D, Barbula fallax; E, Fontinalis antipyretica; F, section of leaf of Leucobryum (B, C, from Goebel after Vaizey; E, after Schimper; F, after Goebel).

(exostome) consists of sixteen teeth. The inner (endostome) is composed of very thin cell membranes. The inner peristome is the homologue of the single peristome of the Haplolepideae.

There is much greater variation in both endostome and exostome in the Diplolepideae than is the case in the single peristome of the Haplolepideae. The endostome in the former may consist of sixteen simple teeth, but in its typical form it shows a basal cylindrical membrane, or collar, which bears on its margin slender filaments (cilia).

There are two main divisions of the Diplolepideae—Epicranoideae and Metacranoideae. In the Epicranoideae the exostome teeth are superposed upon the endostome processes and the exostome teeth are usually undivided. The familiar Funaria hygrometrica belongs to this section of the Eu-Bryales. The Metacranoideae include the majority of the Eu-Bryales. In these the exostome teeth alternate with the endostome processes and are usually undivided. There are many variations in the details of the peristome, which are considered in the classification of this great assemblage of families and genera.

CLEISTOCARPI

In about a dozen genera of the Bryales the capsule does not open by a definite operculum and no peristome is present. The capsule opens irregularly; and these genera have been grouped together as "Cleistocarpi," contrasted with the remaining Bryales, known as "Stegocarpi," which have a definite operculum and peristome. It is generally agreed that this division of the Bryales is an artificial one; but there is still some question as to the relationships of the cleistocarpous genera.

Some of the Cleistocarpi are very much simpler in the structure of both gametophyte and sporophyte than the typical Bryales; and whether these simple forms are really primitive or are reduced from more specialized genera is still a matter of controversy. Among these Cleistocarpi is Archidium, already discussed in the preceding chapter. Aside from Archidium the simplest of the Cleistocarpi are Ephemerum and the very similar Nanomitrium. The former is cosmopolitan, with about thirty species, especially well represented in North America. The protonema here is permanent, and upon it are borne the very short leafy shoots bearing the archegonia or antheridia. The slender crowded leaves may have a midrib or this may be absent. The early development of the embryo, according to Müller, is like that of the typical Bryales. The archesporium arises in the same way, and a lacuna is formed between the outer spore sac and the wall of the capsule.

The archesporial cells are few in number, are correspondingly large, and occupy the greater part of the interior of the capsule, the columella being almost completely obliterated and the large spores completely filling the capsule.

Goebel has described the early stages of the sporophyte in *Nanomitrium*, which is even more reduced in structure than *Ephemerum*; the early stages of the two are much alike.

Some of the Cleistocarpi, e.g., *Phascum* and *Pleuridium*, differ but little from the typical Eu-Bryales up to the later stages of the sporophyte, except for the failure to develop an operculum and a peristome. In most of the cleistocarpous mosses the capsule is sessile, or with very short seta, and the wall breaks irregularly, setting free the large spores. Where a definite seta is present, e.g., in *Phascum*, the ripe capsule becomes detached from the seta and the spores are discharged through the opening thus formed at the base of the capsule. Brotherus regards all the cleistocarpous genera as reduced from stegocarpous types, with which they should be associated. Thus he places *Ephemerum* and *Nanomitrium* in the Funariaceae, *Phascum* in the Pottiaceae, and *Pleuridium* in the Dicranaceae.

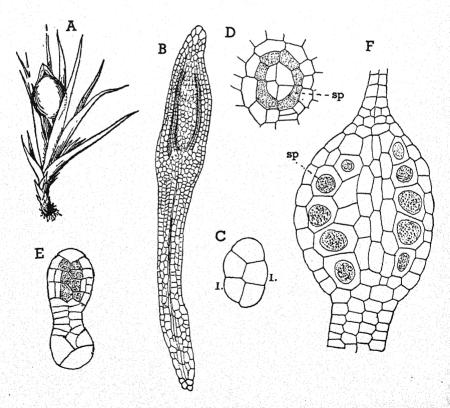


Fig. 105.—Cleistocarpi. A, Pleuridium subulatum; B, section of sporophyte; C, embryo of Phascum cuspidatum; D, cross section of an older embryo; E, embryo of Nanomitrium; F, central region of the young sporogonium of Ephemerum phascoides (E, after Goebel; F, after Müller).

INTERRELATIONSHIPS OF THE MUSCI

It is evident that the Musci constitute a very clearly delimited class, and their relationships with the other bryophytes are, at best, remote. As in the Hepaticae and the Anthocerotes there is a progressive elaboration of the sporophyte which may or may not be associated with a parallel elaboration of the gametophyte. In the Musci both gametophyte and sporophyte reach a degree of specialization far in advance of anything found in the other bryophytes; and although the sporophyte of Anthoceros may rival in size that of the most specialized mosses and like them has developed an efficient photosynthetic system, it is much less specialized, while the gametophyte is an almost undifferentiated thallus. In the mosses the gametophyte seems to have reached the limit possible for such an originally aquatic organism transferred to an aerial environment and the type of structure seems only imperfectly fitted to terrestrial life. The gametophyte of all the archegoniates is more or less amphibious. Free water is essential for fecundation. and not even the most highly developed of the mosses have ever solved satisfactorily the problem of the water supply. They are often capable of enduring long periods of desiccation but remain completely dormant under these conditions, absorbing water when it is supplied much as an alga would do, and even in the largest and most highly developed of the Musci the root system is composed only of rhizoids which would be quite inadequate to provide water necessary to make good the loss by transpiration in a large terrestrial plant; and there is no evidence that any higher land plants have developed from the elaborate leafy gametophytes of such mosses as Polytrichum and Dawsonia. The great development of the gametophyte and its power of rapid asexual reproduction sometimes almost does away with development of the sex organs and of the sporophyte, which, while showing a highly specialized structure and one well developed for photosynthesis, very rarely shows any marked tendency to become independent. Like the gametophyte, it has reached a degree of specialization which apparently marks the end of a definite line of development.

Of the Musci, Sphagnum is generally recognized as the most primitive. There are some significant points of structure between Sphagnum and Anthoceros, indicating a possible remote relationship. The protonema of Sphagnum is a simple thallus, instead of the filamentous type characteristic of the Bryales. It is to be noted, however, that secondary protonemal filaments, arising from the margin of the thallose protonema, exactly resemble the typical moss-protonema. Thallose protonemata also occur in Andreaea and Tetraphis, both considered to be primitive types. This may have a bearing on the phylogeny of the mosses. It is quite conceivable that the filamentous protonema of the higher mosses is secondary and has been derived from some thallose ancestor through Sphagnum or some similar type.

The development of the filamentous protonema is associated with the increasing importance of the leafy shoots developed from it. The filamentous protonema perhaps provides a more rapid production of the leafy shoots than is the case with the thallus, which has been eliminated in the higher mosses.

Some students of the mosses, including Goebel, believe that the filamentous protonema is primitive and indicates a derivation from some filamentous algal ancestors; but the structure of the sex organs, especially the archegonium, and the structure of the sporophyte in even the simplest mosses offer little evidence in favor of this hypothesis. On the other hand, the structures of the reproductive organs and the embryo are sufficiently close to those of the Hepaticae and Anthocerotes to warrant the assumption of a real—if remote—relationship with the less specialized bryophytes. The marked similarlity in the development of the sporophyte of Sphagnum and the Anthocerotes indicates that of the living forms the Anthocerotes approach nearest to the ancestors of the Sphagnales and perhaps, through them, of the higher mosses.

Andreaea is in several respects intermediate between the Sphagnales and the Bryales. The peculiar dehiscence of the capsule in Andreaea has been compared with that of some of the Jungermanniales, e.g., Pallavicinia; but there is little reason to assume any genetic relation between them. It might better, perhaps, be compared with the condition in Tetraphis, although in the latter it is only the inner tissue of the operculum which is thus divided.

Tetraphis has the simplest type of peristome among the Bryales, but the conclusion that from this the more elaborate types found in the Polytrichales and Eu-Bryales have been derived must be accepted with some reservation. Assuming that Tetraphis does connect the Andreaeales with the Bryales, we may recognize the two main phyla: Polytrichales, in which the most highly developed members of the Musci are found; and Eu-Bryales, which constitute the overwhelming majority of the living mosses.

It is questionable whether the Buxbaumiaceae are sufficiently distinct to warrant the establishment of a special order, Buxaumiales. In spite of the greatly reduced gametophyte, the sporophyte shows obvious structural resemblances to that of Dawsonia. In the latter, although its gametophyte is the most highly developed among the Polytrichales, the sporophyte is somewhat simpler than in Polytrichum and the peristome less specialized. The peristome in Buxbaumia originates from a series of concentric cell layers, very much as in Dawsonia, but the peristome teeth are composed of cell membranes only, like the Eu-Bryales. Whether the structure of the peristome in Buxbaumia and the similar condition in Webera (Diphysia) is reduced from the type of Dawsonia is not at all certain; but it

mosses and Anthocerotes there is a very complete photosynthetic apparatus. The great importance in the evolution of the sporophyte of this tendency to "sterilization" of potentially sporogenous tissue has been especially emphasized by Professor F. O. Bower.

Although in the mosses the sporophyte reaches a high degree of specialization, in both the mechanism for the discharge of the spores in the presence of a well-developed conducting tissue and a complete apparatus for photosynthesis, nevertheless in very few cases is there evident any tendency for the sporophyte to sever its connection with the gametophyte. As in the Hepaticae, the discharge of the spores ends the life of the sporophyte. In the mosses the elaboration of the sporophyte is to a certain extent parallel with that of the gametophyte, the most highly developed sporophytes, e.g., Polytrichales, being borne by the most highly developed gametophytes. This may perhaps explain the close dependence of the sporophyte upon the gametophyte.

The mosses have best succeeded in adapting the gametophyte to the varied conditions of terrestrial life and, in some degree, compete successfully with the vascular plants. This may perhaps explain the relative unimportance of the sporophyte in the mosses and the fact that sexual reproduction is so rare in many species which depend almost exclusively upon asexual multiplication.

There is no indication that the mosses, with their highly specialized structures of both gametophyte and sporophyte, have ever given rise to any true vascular plants.

In the Anthocerotes the gametophyte is a simple thallus, comparable to that of the more primitive Hepaticae; but the sporophyte may rival in size that of the larger Musci. The sporophyte, however, is here very much simpler in structure than in the mosses—a simple cylindrical body with a large foot embedded in the gametophyte. There is no differentiation into seta and capsule; but above the foot is the active zone of meristem, adding constantly to the basal tissue of the elongating sporophyte.

In most species of Anthoceros the young sporogenous tissue consists of but a single layer of cells extending to the base of the sporophyte and enclosing an axial cylinder of elongated cells, the columella, which in the earlier stages is probably efficacious in water conduction. The columella, in position and to some extent in function, may be compared to the axial vascular bundle found in some of the simpler vascular plants.

Outside the sporogenous tissue are several layers of chlorophyll cells and in *Anthoceros*, as already indicated, stomata are formed in the superficial layer (epidermis) and thus a definite photosynthetic system is formed. From the sporogenous layer fertile and sterile cells are differentiated, as in the Hepaticae.

Owing to the activity of the meristem above the foot, the growth of the sporophyte continues long after the first spores are discharged and the spore formation does not end the life of the sporophyte as it does in the mosses and Hepaticae. The massive foot encroaches more and more on the gametophytic tissues and there is some evidence that it may sometimes eventually destroy the ventral tissue of the gametophyte and come into direct contact with the substratum, thus freeing the sporophyte entirely from the gametophyte. In Anthoceros, therefore, there is a condition

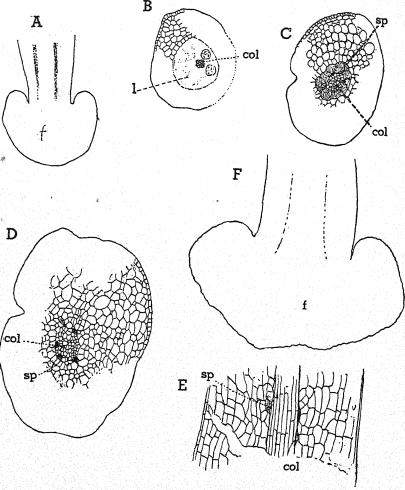


Fig. 107.—A, base of normal sporophyte of Anthoceros fusiformis; B, cross section of the same; col, columella; l, lacuna; C, abnormal sporophyte of A. fusiformis, with greatly enlarged columella, and no lacuna; D, an extreme case, the sporogenous tissue almost completely suppressed; E, longitudinal section of the same sporophyte; F, foot and base of a large specimen, drawn to same scale as A.

which approaches closely what may be assumed preceded the origin of the first true vascular plants.

Normally in Anthoceros, before the spores are ripe, a large lacuna is formed between them and the columella, which dries up as the spores mature. Exceptionally, however, this lacuna is not formed and through a more or less complete suppression of the sporogenous tissue the greatly enlarged columella remains in contact with the green amphithecial tissue, which in this case is much more developed than in the normal sporophyte. These abnormal sporophytes are decidedly larger than the normal ones and the structure is extraordinarily like that of the fossil Rhyniaceae, the simplest known vascular plants.

THE PTERIDOPHYTA

With few exceptions the living pteridophytes may be referred to four classes, viz., Psilotineae, Filicineae, Equisetineae, and Lycopodineae, of which the Filicineae (ferns) are the predominant forms.

Our knowledge of the fossil bryophytes is so scanty that a study of their phylogeny must depend largely upon a comparative study of the living forms; in contrast, the vascular plants have left abundant and often perfectly preserved fossil remains, which throw much light upon their early history. Of special interest is the discovery of very simple vascular plants in the Devonian rocks of Great Britain and Germany and, more recently, in the United States.

The simplest known vascular plants, the Rhyniaceae, were first described by Kidston and Lang from Devonian rocks in Scotland.¹ Two genera, Rhynia and Hornea, were recognized. The sporophyte in the Rhyniaceae does not show the definite organs, viz., stem, leaf, and root, found in "typical" vascular plants. The first species described, Rhynia Gwynne-Vaughnii, was a leafless plant, sometimes dichotomously branched. The upright shoot arose from a prostrate rhizome structurally much like the upright shoot. In the second genus, Hornea, the "rhizome" is a tuberous body having no vascular bundle and very suggestive of the large foot of Anthoceros.

Zimmermann has proposed for such a generalized, dichotomously branched plant body the term "telome," and this is applied also to the branches of a telome system. The ultimate branches of a telome system may be either sporogenous (sporangiophores) or sterile (phylloids).

The shoot in Rhynia has a central vascular bundle with a core of woody elements (xylem), the rest of the shoot being composed of undifferentiated

¹ Some fossils, apparently of vascular plants, have been reported from Silurian rocks in Australia. One of these, *Baragwanthia longifolia*, much larger than the Devonian Rhyniaceae, had numerous slender leaves, which Lang compares with *Lycopodium*.

thin-walled cells. In the more slender shoots the xylem may be reduced to two or three tracheids or may even be quite absent from the smallest branches. The sporophyte of the *Rhynia* is not much advanced beyond the largest known type of *Anthoceros*, and the resemblance in *Hornea* is even more striking. Indeed the latter has been described by Seward "as little more than a slightly ramified and free-growing *Anthoceros*."

A section of the sporophyte of the largest known Anthoceros differs from a similar section of Rhynia only in the absence of tracheary tissue. In the lower part of these larger sporophytes the sporogenous tissue may

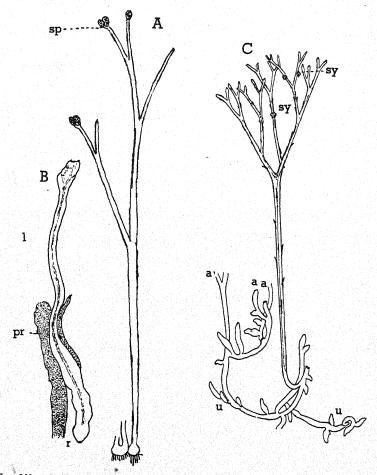


Fig. 108.—A, Hornea, restoration of a primitive vascular plant from the Devonian; sp, sporangia; B, young sporophyte of Ophioglossum moluccanum, composed of leaf and root only; pr, the gametophyte; C, Psilosum triquetrum; u, the subterranean rhizome; sy, synangium (A, after Kidston and Lang; C, after Bertrand).

be almost entirely suppressed and there is a decided increase in the green amphithecial area. A section shows a conspicuous central cylinder of presumably conducting cells, comparable to the central vascular bundle of *Rhynia*. Surrounding this primitive vascular bundle (stele) is a massive zone of chlorophyllous cells (cortex), and the epidermis has definite stomata like those of the typical vascular plants.

The similarity of structure between the Rhyniaceae and the Anthoceros forms already referred to is quite remarkable, and this resemblance is further increased when the sporogenous structures are compared. In the Rhyniaceae the spores are formed at the apex of some of the branches. The

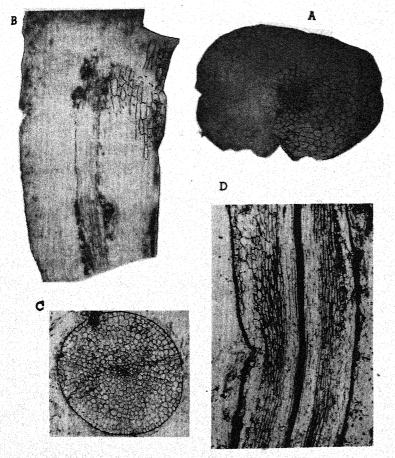


Fig. 109.—A, cross section, B, longitudinal section of sporophyte of the larger Anthoceros; C, D, similar sections of Rhynia (A, B, photographs by Dr. D. A. Johansen: C, D, after Zimmermann).

mass of spores is separated from the epidermis by several layers of cells, and the branch tip thus forms a very primitive type of "sporangium." A longitudinal section of the sporangium shows that the spores form a thick layer overarching a central columella, much as in the moss Sphagnum or the Anthocerotaceae. The resemblance is especially marked when comparison is made with some of the simple Anthocerotaceae, especially Notothylas.

From a study of these earliest known vascular plants and their obvious resemblances to the Anthocerotaceae, which among living bryophytes have the sporophyte most nearly approaching the independent condition characteristic of the pteridophytes, it is justifiable to conclude that the ancestors of the first vascular plants, if not actually Anthocerotes, were at any rate forms which must have closely resembled them.

There is good reason to believe that the Anthocerotes are very old types. The gametophyte more nearly resembles the green algae than does that of any other archegoniates. On the other hand, the sporophyte becomes more nearly independent than that of any other bryophyte and, except for the absence of tracheary tissue and lack of branching, can readily be compared with the undifferentiated telome of the Rhyniaceae. It is quite conceivable that, like the still more ancient ancestors of the higher plants, the green algae, the Anthocerotes are the little-changed descendants of plants that flourished long before the advent of the first vascular plants.

Probably related to the Rhyniaceae, but somewhat more specialized, are a number of other Devonian fossils, some of which seem to foreshadow the principal classes of the living pteridophytes. Especially important contributions to our knowledge of these forms have been made by Professor R. Kräusel and others from fossils which were discovered in the Rhine Valley. Other important discoveries have been made in Britain by Kidston and Lang. One of these fossils, <u>Asteroxylon</u>, has dichotomously branched shoots arising from a prostrate rhizome, much like some species of Lycopodium and having a much better developed vascular bundle (stele) than the Rhyniaceae and comparable with that in Lycopodium. The shoots were covered with closely set, small, leaf-like appendages. The sporangia, however, were terminal bodies, very different from those of Lycopodium.

The forked telome of the Rhyiaceae shows both fertile and sterile branches. By repeated dichotomy in one plane such a plant body would result in a fan-shaped structure not clearly differentiated into stem and leaf but forming a "frond" and recalling the leaves of such ferns as Schizaea dichotoma, Dipteris, or Matonia. It is possible that the predecessors of the modern ferns may have been similar to the Devonian Hyenia and Cladoxylon. Calamophylon, also a Devonian type, suggests a possible relationship with the horse-tails (Equisetineae).

One living family, however, the Psilotaceae, show such marked resemblances to the Rhyniaceae that their inclusion with them in the Psilophyta is probably warranted. This term was proposed to include the Rhyniaceae and the other Devonian genera which seem to be related to them. We propose here to use Psilophytineae to denominate the class, rather than Psilophyta. The type of the class is *Psilophyton*, a Devonian fossil of wide distribution. *Psilophyton*, as well as several others of the class, were discovered in lower Devonian rocks in Wyoming in 1932 by Dorf. Among his discoveries was a new form, *Bucheria ovata*, which shows some interesting resemblances to the Ophioglossales.

The only living representatives of the Psilophytineae belong to the small family Psilotaceae, with about a half-dozen species. There are two genera—Psilotum and Tmesipteris—the first represented in most tropical

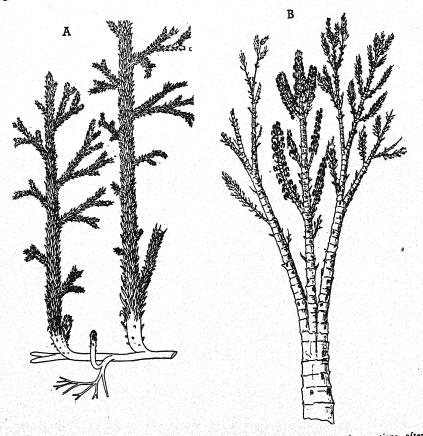


Fig. 110.—Devonian Psilophyta. A, Asteroxylon; B, Calamophyton (restorations after Kräusel and Weyland).

and some warm-temperate regions. The sipteris occurs only in Australia and New Zealand and some of the Pacific Islands. Psilotum triquetrum occurs in most tropical and subtropical regions, including Florida and South Carolina. The plant, which often grows in exposed rocky localities, requires moisture and humus for the growth of the extensively branched rhizomes which penetrate the crevices of the rocky substratum. As in the Rhyniaceae, there are no true roots. From the rhizome arise upright aerial shoots, which branch dichotomously much as in the Rhyniaceae. There are only minute scale-like leaves, and the shoot might be called a "telome," since, as in Rhynia, there is no differentiation into stem, leaf, and root. Another species, P. flaccidum, is an East Indian epiphyte with pendent flattened branches. The spores in Psilotum are produced by a short "sporangiophore," which probably represents a branch bearing three masses of

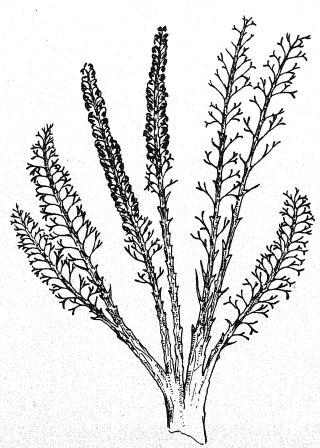


Fig. 111.—Devonian Psilophyta, Hyenia (restoration after Kräusel and Weyland).

spores at the apex comparable to the single terminal sporangium of *Rhynia* but more definite, and perhaps best called a trilocular synangium. This synangium is subtended by a pair of leaves or perhaps a single bifid leaf or bract.

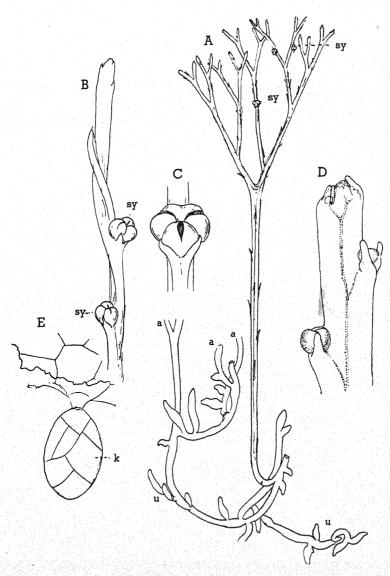


Fig. 112.—Psilotum. A, P. triquetrum, habit; B, branch, with synangia, sy; C, synangium, showing dehiscence; D, P. flaccidum; E, gemma from rhizome (A-C, after Bertrand; D, after Goebel; E, after Solms-Laubach).

The growth of the branches is from a definite apical cell, much like that in most ferns. The branching is a true dichotomy resulting from the obliteration of the original apical cell and the formation of new initials for the two branches.

There are numerous stomata in the epidermis, below which is a zone of green tissue, the essential photosynthetic tissue, as the leaves are rudimentary. Within the green tissue is a zone of thick-walled cells (sclerenchyma), the principal strengthening tissue of the shoot. The center of the shoot is occupied by the stele, having a core of sclerenchyma, from which radiate several bands of tracheary tissue, or xylem. The phloem is not well differentiated. There may be as many as ten of the xylem masses. Seen in cross section the radiating xylem masses form a star-shaped mass with the small primary tracheids (protoxylem) at the outer points and the larger secondary xylem developed centripetally. The phloem between the xylem masses is poorly developed and its limits are impossible to determine with certainty.

Rapid multiplication in *Psilotum triquetrum* may result from gemmae formed by the rhizome. From these are developed elongated subterranean shoots composed of uniform parenchyma, but later having an axial vascular bundle. These finally develop into typical rhizomes from which later the aerial shoots are produced.

Tmesipteris tannensis is not uncommon in Australia and New Zealand. where it is usually an epiphyte, often attached to the trunk of tree ferns. It reaches its best development in the very humid regions of western and southwestern New Zealand. Holloway states that in these regions the pendent shoots may reach a length of two to four feet. In such forms there are alternating zones of sporangiophores and leaves; but in some of the smaller types, with semi-erect shoots, the whole terminal portion is fertile. Tmesipteris is usually epiphytic, on the trunks of tree ferns, especially Dicksonia squarrosa, but also occurs on moss-covered trees and the heaps of humus at their bases. The rhizome is dichotomously branched and the ends of the branches develop into the aerial shoots, which are generally unbranched but may sometimes show a single dichotomy. The shoots are usually pendent, like those of Psilotum flaccidum, but differ from the latter in having large leaves. The leaves first formed are rudimentary, like those of Psilotum, but the later ones are conspicuous. They are in two to five irregular rows, and are vertical like the phyllodia of some Acacias or the "cladodes" of Ruscus. Sahni, who has investigated the structures of the leaf in another species, T. Viellardi, thinks that the vertical leaves of Tmesipteris are not homologous with the leaves of the higher plants and calls them "prominent wings" on the axis, each decurrent through many nodes. He thinks that the stem appears to be entirely composed of concrescent leaf bases, "affording a striking illustration of the phytonic theory." It may be that just as the line between root and shoot is very vague in the Psilotales, the subterranean shoots functioning as roots, so the "leaves" in *Tmesipteris* may also have an intermediate character and the vascular system of the axis may be made up of a fusion of leaf traces. The xylem masses are much like those in *Psilotum* but are less symmetrically arranged. The leaves have a well-developed vascular bundle, which extends as a leaf trace into the axis and joins the central vascular cylinder.

T. Viellardi, a normally upright terrestrial species, is a more robust plant than T. tannensis and has a more complex vascular system. A cross

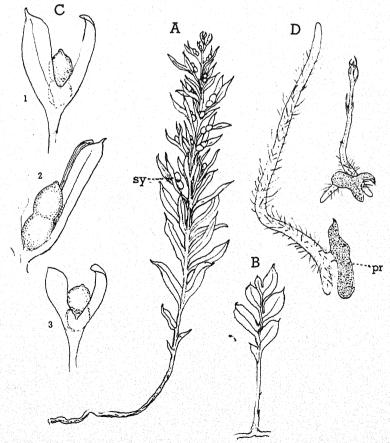


Fig. 113.—Tmesipteris. A, T. tannensis, with synangia, sy; B, young plant of T. Viellardi; C, synangia of T. tannensis; D, gametophytes of T. tannensis, with attached sporophytes (A, C, after Sykes; B, after Sahni; D, after Holloway).

section of the shoot in the leafy region shows a central pith surrounded by a zone of collenchyma, outside of which is a ring of xylem masses about twice as numerous as in *T. tannensis*. These xylem masses are apparently made up entirely of the fusion of individual leaf traces. Unlike *T. tannensis*, *T. Viellardi* has a single central vascular strand in the pith—presumably the continuation of the xylem of the stele of the rhizome, which is continued with little change into the aerial shoot.

In all of the Psilotaceae there is found an endophytic fungus such as occurs in many other plants, notably those growing in humus soils and presumably, to a certain extent, of saprophytic habit. The presence of humus is evidently essential for normal growth in the Psilotaceae. The rhizome in *Tmesipteris* was examined by Miss M. G. Sykes. It shows a definite apical cell, and rhizoids are formed from some of the epidermal cells. Below the epidermis is the cortex composed of several cell layers, some of which form a well-defined zone containing the endophytic mycorrhiza associated with the saprophytic habit of the plant. The vascular bundle (stele) shows a definite bundle sheath (endodermis) and consists of a central core of xylem surrounded by poorly differentiated phloem. The structure of the rhizome in *Tmesipteris* thus resembles very closely that of the aerial shoot of *Rhynia*.

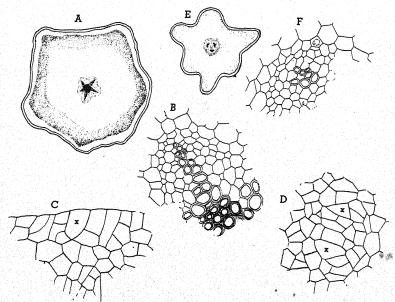


Fig. 114.—Psilotaceae. A, section of stem of Psilotum triquetrum; B, part of central cylinder, more enlarged; C, apical cell of Psilotium; D, apex of rhizome showing dichotomy; E, section of stem of Tmesipterus tannensis; F, part of central cylinder more enlarged (C, D, after Solms-Laubach).

THE SPORANGIOPHORE

There has been marked disagreement as to the morphological nature of the sporangiophore in the Psilotaceae. A number of investigators, especially Bower, regard the sporangiophore as a foliar structure—a "sporophyll" comparable to that of Lycanodium. Other eminent botanists, e.g., Sachs, Strasburger, and Goebel, have held that the sporangiophore is a fertile branch. Miss Sykes, in her investigation of Tmesipteris, inclines to the latter view. The writer, who formerly accepted the foliar theory, now believes, especially in view of the discoveries of the Rhyniaceae, that the synangium of the Psilotaceae is the equivalent of the fertile shoot (sporangiophore) of the Rhyniaceae.

Goebel more recently is inclined to accept Professor Bower's interpre-

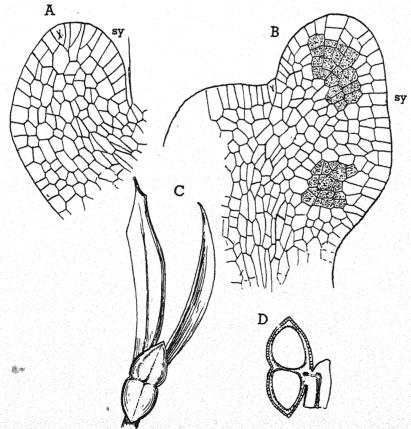


Fig. 115.—Tmesipteris tannensis. A, section of young sporangiophore; sy, synangium; B, older stage, sporogenous areas shaded; C, sporangiophore with bilocular synangium; D, section of synangium (all figures after Bower).

tation of the sporangiophore as a sporophyll but admits that there is ground for the interpretation of the sporangiophore as a branch structure. His figures, in his *Organographie*, of the position of the sporangiophore in both *Tmesipteris* and *Psilotum*, especially *P. flaccidum*, suggest that, in accordance with the predominant dichotomous branching in *Psilotum*, the sporangiophore is the result of an unequal dichotomy of the shoot apex, one branch continuing the growth of the main shoot, and the other remaining short and bearing the synangium. This would correspond to the formation of fertile and sterile branches of a telome, as in *Rhynia*.

The development of the synangium has been studied in detail by Bower and is essentially alike in the two genera. The synangium is at first composed of a mass of uniform tissue. Later, at two points in *Tmesipteris* and three in *Psilotum*, masses of sporogenous tissue develop, but it is not certain that each of these masses can be traced to a single arche-

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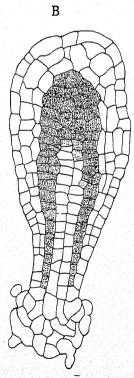


Fig. 116.—A, sporangium of Hornea; B, young sporogonium of Notothylas javanicus, the sporogenous tissue shaded (A, after Zimmermann).

sporial cell. The groups of spores are separated from the epidermis by several layers of cells which form the outer wall of the chamber (loculus). The number of sporogenous cells in each loculus is large, but some of them become disorganized, and only a part of them undergo division into the spore tetrads. Each loculus opens by a longitudinal cleft.

THE GAMETOPHYTE

The gametophyte of the Psilotaceae was quite unknown until 1914, when Professor A. A. Lawson discovered in Australia gametophytes of both *Psilotum* and *Tmesipteris*. Soon afterward Dr. J. E. Holloway described the gametophyte and embryo of *Tmesipteris* collected in New

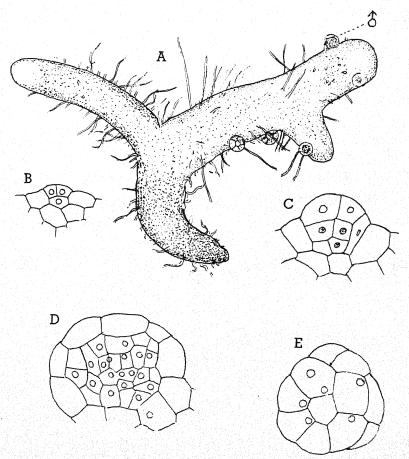


Fig. 117.—Tmesipteris tannensis; A, gametophyte, with antheridia, &; B, C, young antherida; D, an older antheridium; E, surface view of antheridium (B-E, after Holloway).

Zealand and in 1921 published a very complete account of the embryo. The general structure of the gametophyte is much the same in the two genera.

The gametophyte is a subterranean, somewhat branched, cylindrical body, destitute of chlorophyll and brownish in color. In general appearance it resembles the rhizome of the sporophyte, and like it grows in soil containing humus. Numerous rhizoids grow from the surface, and a section of the gametophyte shows the presence of the same endophytic mycorrhiza which occurs in the rhizome. The cells containing the endophyte, however, are irregularly scattered through the section. Archegonia and antheridia are borne in large numbers on the same individual, but they are not confined to any special region. Both archegonium and antheridium are much more like those of some of the ferns than like the Lycopods, with which the Psilotaceae have often been associated.

Holloway recently announced the discovery of tracheary tissue in the larger gametophytes of *Tmesipteris*. ? Peilotan

The antheridium is formed from a superficial cell, which first divides into an outer and an inner cell, the latter by repeated division forming the mass of spermatocytes. The young antheridium soon forms a hemispherical protuberance, and when full grown is nearly globular in form and superficially very much resembles that of the common ferns (Leptosporangiatae). In this respect the Psilotaceae differ from the other pteri-

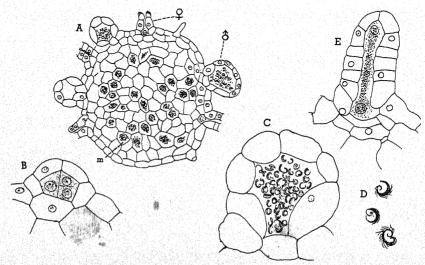


Fig. 118.—Psilotum triquetrum. A, cross section of gametophyte; \mathcal{C} , antheridia; \mathcal{C} , archegonia; m, mycorrhiza; \mathcal{B} , young, \mathcal{C} , older antheridium; \mathcal{D} , spermatozoids; \mathcal{E} , archegonium (all figures after Lawson).

dophytes in which the mass of sperm cells is embedded in the gameto-phyte. The details of spermatogenesis have not been investigated but probably do not differ essentially from those of the other forms that have been studied. Lawson found that the spermatozoids of *Psilotum* are multiciliate, like those of the ferns and horse-tails (*Equisetum*). Presumably *Tmesipteris* will also show similar spermatozoids.

The ripe antheridium has a large number of sperm cells, and the wall is composed of about a dozen cells, one of which serves as an operculum. Among the ferns the antheridia of the more primitive leptosporangiate genera, e.g., *Gleichenia* and *Osmunda*, most nearly resemble those of the Psilotaceae. The archegonium has a conspicuous straight neck and in general form and structure also resembles the lower leptosporangiates.

THE EMBRYO

The development of the embryo has been investigated by Holloway in *Tmesipteris*. There is evidently considerable variation in the early divisions. The first division (basal wall) in the zygote is transverse, as in most bryophytes; and from the lower (hypobasal) cell is developed a conspicuous foot. The epibasal portion of the embryo develops into a conical body, and the young sporophyte at this stage bears a striking resemblance to that of *Anthoceros*. This resemblance is increased by the

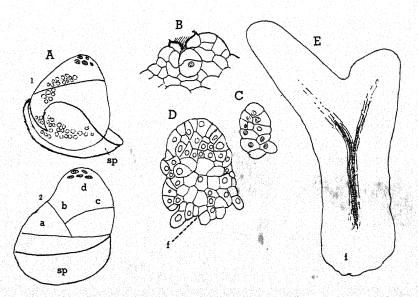


Fig. 119.—A, germinating spores of *Psilotum*; B, D, young embryos of *Tmesipteris*; E, young sporophyte showing first fibro-vascular bundles; f, the foot (A, after Darnell-Smith; B-E, after Holloway).

root-like extensions of some of the superficial cells of the foot. In one important particular, however, the embryo differs from that of *Anthoceros*, in developing at an early stage a definite apical cell. A second similar cell is developed somewhat later and the young sporophyte soon shows two diverging branches, sometimes alike, sometimes unequal. At an early stage a vascular bundle is developed in each of the branches which unite at the base to form a single axial stele.

These two branches ramify through the substratum and contain the characteristic endophytic fungus found in the gametophyte, which the young sporophyte resembles in general appearance, and like it has numerous rhizoids covering its surface. The primary shoots are entirely subterranean and may reach a length of half an inch or more before developing the first aerial branch. Usually one of the two primary branches turns upward and emerges as the first aerial shoot, and the other continues to extend through the humus substratum to form the permanent rhizome.

The primary aerial shoot is at first destitute of any leaves or scales and is more slender than the subterranean rhizome. The first leaves to develop are small scales and are followed by successively more developed ones. The shoot remains slender and does not form sporangiophores. It seldom is more than an inch or two in height, and the leaves are in two series. The fully developed leafy shoots, which may sometimes show a single dichotomy, have the leaves in three to five rows.

THE RELATIONSHIPS OF THE PSILOTACEAE

The Psilotaceae formerly were usually regarded as most nearly related to the Lycopodineae. The sporangiophore was considered as a "sporophyll" bearing a synangium, instead of the simple sporangium of Lycopodium. As the result of more critical investigations a number of investigators concluded that the nearest relatives of the Psilotaceae were the Sphenophyllales—characteristic fossils, especially in the Carboniferous. Lawson also expressed his belief that this relationship with the Sphenophyllales is warranted. Sahni thinks there may be some remote relation of the Psilotaceae to both Lycopodineae and Sphenophyllales. The latter, however, differ markedly in their general structure from the Psilotaceae: the stems are jointed, and the leaves are in whorls at the nodes of the stem. In these respects, as well as some others, the Sphenophyllales would seem to show evidences of nearer relationship with the Articulatae (Equisetineae).

Holloway recognizes the marked similarity of the embryo of *Tmesipteris* to that of *Anthoceros*, and also indicates that in the young sporophyte of *Tmesipteris* there is a marked approach to the condition in *Rhynia*. The undifferentiated young sporophyte of *Tmesipteris* is therefore to be con-

sidered as primitive and not secondary. The evidence that the sporangiophore of the Psilotaceae is really a branch, the result of an unequal dichotomy of the shoot apex, seems fairly convincing.

The relationship with the Sphenophyllales has been rejected by Miss Sykes, as a result of her investigations in *Tmesipteris*. She concludes that the Psilotaceae should be separated from the other pteridophytes as a distinct order. The discovery of the Rhyniaceae and the final discovery of the gametophytes of the Psilotaceae show such evidences of a real relationship as to warrant their being placed in a special class, Psilophyta or Psilotineae, co-ordinate with the three other classes of the pteridophytes, viz., Lycopodineae (Lycopsida), Equisetineae (Articulatae), and Filicineae (Pteropsida). There is some evidence that these three classes may have been derived from some of the Devonian Psilophyta.

The saprophytic habit of the gametophyte of the Psilotales brings up the question as to the origin of this condition which is present in the subterranean gametophytes of some of the other presumably primitive pteridophytes, viz., Lycopodiaceae and Ophioglossaceae. What the condition was in the Rhyniaceae it is, of course, impossible to state.

Should there be a real relationship between the Psilotaceae and Anthoceros, a certain parallelism might be found in the fact that symbiosis is a regular feature in the Anthocerotes—although the symbiont in this case is a blue-green alga and not a fungus. The mycorrhizal fungi, so common in a host of humus plants, may have established this association at a very early period in the evolution of the vascular plants. It is possible that some evidence of this might be found in the petrified tissues of some of the early fossils.

The three classes, Lycopodineae, Equisetineae, and Filicineae, can all be traced back to the Devonian, and became greatly developed in the later Paleozoic, especially the Carboniferous. The ferns have maintained an important place in the floras of the moister regions of the temperate and tropical zones, but the Lycopods and the Equisetineae are now greatly reduced in size and numbers, the latter being reduced to a single genus. It is possible that some of the middle Devonian fossils, like Asteroxylon, Calamophyton, and Hyenia, might be considered as generalized types connecting Psilophyta and the existing pteridophytes.

From the dichotomously branched telome of the Rhyniaceae the further differentiation of the sporophyte seems to have developed along two lines: In one the result was a dichotomously branched axis, bearing many small leaves and having a massive axial fibro-vascular cylinder, or stele. This type, shown in Asteroxylon, may connect with the microphyllous Lycopodineae. In another direction it is possible that the ferns (Filicineae, Pteropsida) and the Equisetineae (Articulatae) may also have

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been derived from the primitive Psilophyta. In spite of the very great difference in habit between the existing ferns and horse-tails, there is a possibility of a remote relationship between the latter and the most primitive ferns. The repeated dichotomy in a single plane of a telome like that of the Rhyniaceae and a flattening of the branches would result in a fanshaped frond, like that found in a good many ferns, e.g., Dipteris and Matonia, and the first leaf in most ferns almost always is dichotomous

It is possible that some of the Devonian forms like Hyenia and Cladoxylon might resemble the precursors of the modern ferns. Resembling Hyenia in general form is another remarkable Devonian genus, Calamophyton described by Kräusel. In this genus the main branches are distinctly jointed and bear at the nodes whorls of small forked phylloids, or sporangiophores comparable to those of the living Equisetum. In short, it is quite conceivable that from forms similar to Cladoxylon and Calamonhy. ton there developed in one direction the typically megaphyllous and primarily monophyllous ferns: in another direction, the primitive Articulatae like Archaeocalamites, with jointed stems and whorls of dichotomously divided leaves.

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CHAPTER X

LYCOPODINEAE (LYCOPSIDA)

Except for the Psilotaceae and perhaps the Isoetaceae, all of the existing pteridophytes may be referred to one of the three classes, Lycopodineae (Lycopsida); Equisetineae (Articulatae); Filicineae (Pteropsida). The latter, which comprises the ferns, includes a large majority of the living pteridophytes. The Equisetineae at present have but a single genus, Equisetum, with about twenty-five species. These are the common "horse-tails" or "scouring rushes." The Lycopodineae in point of numbers are intermediate between the horse-tails and the ferns.

The existing Lycopods and Equisetaceae are evidently relicts of the large assemblage of forms related to them which flourished during the Paleozoic era, especially in the Carboniferous. Many of these fossils are much larger and more highly developed than their modern relatives; but among the earlier forms were smaller and simpler types which were probably more nearly related to the living genera, Lycopodium and Selaginella, than the latter are to the later, highly specialized genera, like Lepidodendron and Sigillaria.

In the Devonian and Lower Carboniferous a number of fossils occur which show some evidence of relationship with the existing Lycopodineae; but these are still too imperfectly known to make their relationships, certain. Some of these fossils have been called *Lycopodites* and *Selaginellites*, according to indications that they are, respectively, "homosporous" or "heterosporous." It is also an open question whether these primitive Lycopods may have been derived from forms like the Devonian Rhyniaceae through types like *Asteroxylon*.

The existing Lycopodineae include two families, Lycopodiaceae and Selagin leae, each representing an order. The first has about one hundred species, all but one, *Phylloglossum Drummondii*, belonging to the genus *Lycopodium*, which, however, should probably be separated into several genera. The Selaginellaceae includes some six hundred or more species of *Selaginella*.

The Lycopodiaceae are homosporous, i.e., all the spores are alike and produce large gametophytes, usually bearing both male and female gametangia. The Selaginellaceae are markedly heterosporous, having the small spores (microspores) developing greatly reduced male gametophytes and the large spores (megaspores) from which the female gametophyte is developed.

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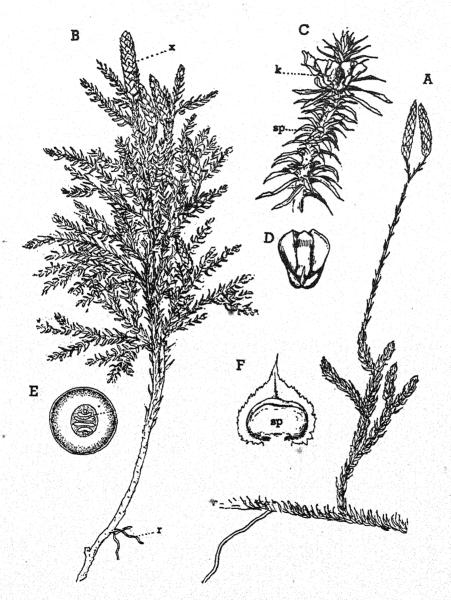


Fig. 120.—A, Lycopodium clavatum; B, L. obscurum, var. dendroideum; C, L. lucidulum; sp, sporangia; k, gemmae; D, gemma of L. lucidulum; E, section of stem of L. obscurum; F, sporangium of L. obscurum.

The Lycopodineae are most abundant in the tropics, but both Lycopodium and Selaginella are cosmopolitan Lycopodium is represented by a number of common species in the northern parts of both hemispheres, and a few species of Selaginella, e.g., S. apus and S. rupestris, are found as far north as New England.

All of the northern species are terrestrial, and most of the species of Lycopodium have a prostrate rhizome from which arise upright shoots, bearing many small leaves, with a single median vascular bundle. The leaves in Lycopodium are most commonly arranged spirally, in several series, but may sometimes be in definite whorls, e.g., L. verticillatum and L. cernuum. Both arrangements may occur in the same species. In most species of Selaginella the shoot is dorsi-ventral, with four series of dorsal leaves, two large and two small. The same arrangement of leaves occurs also in a few species of Lycopodium, e.g., L. volubile.

While most species are terrestrial there are a good many epiphytic ones in the warmer parts of the world. In the terrestrial species of Lycopodium there is generally a creeping stem from which upright leafy shoots are developed. In some of the simplest forms, like L. Selago and L. lucidulum, there is no rhizome, and leafy shoots may be undivided or forked once or twice. The branching in all the species is typically dichotomous; but in some species, e.g., L. obscurum (and L. cernuum), there is a central main axis which grows in length for a considerable time and bears lateral branches which show repeated dichotomy. The lateral branches are generally supposed to arise monopodially; but it is possible that they may be the result of an unequal dichotomy, one branch continuing the main axis, the other forming a branch. In the tropics the pendant branches of epiphytic species like L. phlegmaria and L. squarrosum are characteristic features of the rain forest. From the rhizome roots are formed, usually in acropetal succession, but adventitious roots may also occur.

The species of Lycopodium are usually of moderate size, seldom exceeding a foot in height; but the upright shoots of L. cernuum may be five or six feet high, and the climbing stems of L. volubile may reach a length of thirty feet or more.

The sporangium of Lycopodium is borne on the upper surface of a sporophyll, near its base. The sporophylls may not differ essentially from the sterile leaves or they may be reduced in size and destitute of chlorophyll—forming a scale. Where the sporophylls are like the sterile leaves they may occur at almost any point on the axis, and sometimes groups of these sporophylls alternate with zones of sterile leaves. In most species, however, the sporophylls are scale-like and are confined to the apex of a shoot or branch, generally forming a definite cone or "strobilus."

The stems.—The anatomical structure of the stem is much the same in

all of the species. Occupying the axis is a massive cylinder or stele, sharply marked off from the cortical region by the bundle sheath (endodermis). Within the endodermis is the "pericycle" composed of several layers of cells. There is a good deal of variation in the arrangement of the xylem and phloem elements. In some cases, e.g., *L. cernuum*, a cross section of the stele shows irregular scattered groups of tracheary tissue embedded

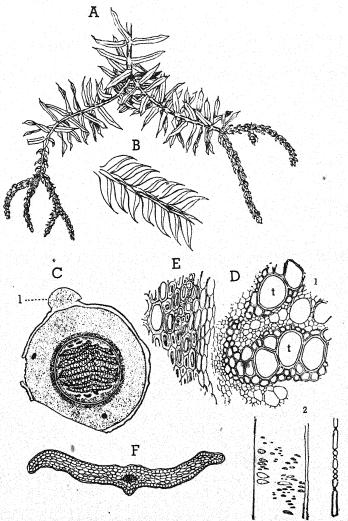


Fig. 121.—A, Lycopodium pachystachyon; B, L. volubile, showing two forms of leaves; C, cross section of stem of L. volubile; D, 1, details of stem tissues; t, tracheids; s, sieve tubes; D, 2, longitudinal section of sieve tubes; E, sclerenchyma from cortex; F, section of leaf of L. lucidulum.

in a ground mass of phloem. In most species the xylem forms very definite plates, symmetrically arranged. In the upright shoots a cross section shows a radial arrangement with xylem and phloem alternating. Sometimes there is a fusion of the xylem plates toward the center, so that in cross section a solid star-shaped xylem appears.

Where the stem is dorsi-ventral in structure, as in the prostrate rhizomes, the section shows a series of parallel xylem masses with the phloem between. The growth of both xylem and phloem is centripetal, the primary xylem elements (protoxylem) being at the periphery. The protoxylem consists of narrow spiral and annular tracheids, while the secondary 97 wood ("metaxylem") is composed of much larger scalariform elements. In the phloem are large sieve tubes, with the characteristic sieve plates.

The structure of the stele in Lycopodium is certainly suggestive of the fossil Asteroxylon, and might perhaps be used as an argument in favor of a definite relationship.

The leaf.—The leaves of all species of Lycopodium are relatively small. sessile, and usually lanceolate in outline. There is a median vascular bundle. which is "concentric," having a central strand of narrow annular and spiral tracheids surrounded by a zone of phloem composed of parenchyma with scattered narrow sieve tubes. The green tissue or "mesophyll" is composed of uniform cells with small intercellular spaces. There is little difference between the epidermis of the upper and lower sides of the leaf, and stomata are usually equally developed on both surfaces.

The root.—In Lycopodium the roots originate much as in most vascular plants, i.e., from the endodermis of the vascular bundle, and break through the overlying tissue. Exceptionally, as in the primary roots of L. cernuum, the root is "exogenous," i.e., formed superficially; and the same has been noted for Phylloglossum. The roots branch dichotomously, the successive forkings being usually in planes at right angles to each other.

The anatomy of the root resembles that of the stem. The stele has six to ten radial xylem plates, sometimes joined at the center of the stele. The primary and secondary tracheids are like those of the stem bundle. Thus while true roots are formed in Lycopodium, their structure is almost identical with that of the stem. This is a step in advance of the condition in the Psilotineae, where no true roots occur, these being replaced by the subterranean rhizome.

Gemmae.—In some species of Lycopodium special buds or gemmae are found, e.g., in L. lucidulum and L. Selago. These gemmae are short branches formed in the axils of the leaves. They consist of a short axis bearing several thickened fleshy leaves. Before becoming detached a root is formed at the base and when the gemma comes in contact with the ground the root quickly fastens the young plant to the substratum.

None of the species of Lycopodium as yet investigated show a definite apical cell in the stem such as is characteristic of the Psilotaceae. The apex of the shoot is broad and only slightly convex, with the central region occupied by a group of apparently similar initial cells. From these initials, lateral segments are cut off which contribute to the cortex and epidermis of the shoot. From the inner faces of the initials segments are formed from which develop the tissues of the massive central stele.

The leaves arise as conical outgrowths of the peripheral region of the apical meristematic area. At an early stage a median strand of narrow cells (procambium) is formed in the young leaf, and this procambian strand forms the midrib of the leaf. It is continued into the cortex of the stem, as a "leaf trace," and finally joins the central vascular cylinder of the stem. A section of the older stem, therefore, shows two distinct systems of vascular bundles—the central cauline stele and the independent leaf traces.

In the root the primary tissues cannot all be traced back to a single group of initial cells. The young epidermis (dermatogen) forms a continuous layer, above which is a layer of meristem (calyptrogen), which contributes to the growth of the root cap covering the growing point of the root. Below the dermatogen is the "periblem," from which are derived the tissues of the cortex; and finally occupying the axis of the root is the "plerome," the young stele, whose growth is due entirely to a group of initial cells at its apex.

As the root grows, from some of the young epidermal cells a wedgeshaped cell is cut off, which divides into two, each part forming a root hair.

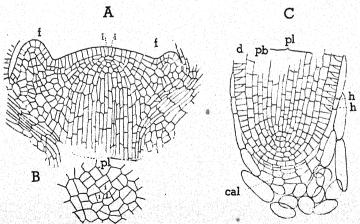


Fig. 122.—Lycopodium Selago; A, stem apex; i, initial cells; B, surface view of stem apex; C, root apex; cal, root cap (all figures after Strasburger).

The sporangium.—The sporangium in Lycopodium is a kidney-shaped capsule attached to the upper surface of the sporophyll near its base, or less commonly growing from the stem close to the leaf base. In such species as L. Selago and L. lucidulum, where the sporophytes do not differ ma-

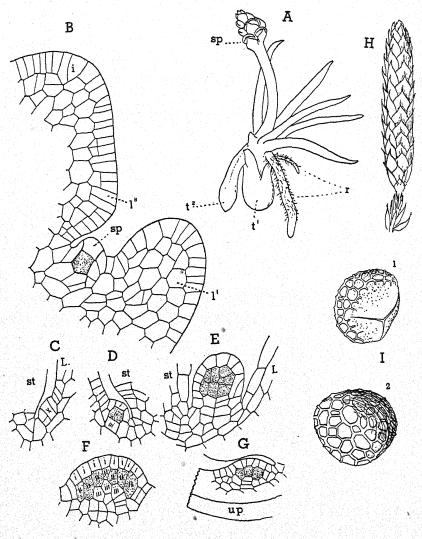


Fig. 123.—A, Phylloglossum Drummondii; sp, sporangia; t, protocorm; r, root; B, longitudinal section of young strobilus of Phylloglossum; sp, young sporangium; l, young sporophylls; C-E, radial sections of young sporangia of Lycopodium Selago; F, G, tangential sections of young sporangia of L. clavatum; H, strobilus of L. obscurum; I, spores of the same. (A, after Bertrand; B-E, after Bower).

terially from the sterile leaves, two types of leaves may be intermingled, the sporophylls may develop at any point, and the further elongation of the shoot is not affected. An advance on this condition is seen in the *L. inundatum* and some allied species, where, although the sporophylls are much like the sterile leaves, they are restricted to the apex of the shoot, where they form a lax strobilus. In most of the species, however, the sporophylls are broad scales which are closely imbricated and form the conspicuous cone at the end of the shoot. The latter may be elongated below the cone, or the leaves may be reduced to small scales, so that the strobilus is borne on a sort of elongated pedicel.

Professor F. O. Bower has studied in detail the development of the sporangium in a number of representative species of Lycopodium. The simplest type is that of L. Selago, one of the least specialized forms, in which the sporophyll resembles the ordinary leaves. The young sporangium is a slightly elevated transverse ridge at the base of the sporophyll. A radial section in the earliest stage shows a single cell, but this is really only one of a series of cells forming the young sporangium. Each cell of this primary row divides into a large central cell and two lateral ones. The central cell is then divided transversely into three, of which the middle one, together with the corresponding ones in other parts of the sporangium, forms the "archesporium" or sporogenous region. The superficial cells, by further periclinal divisions, become the sporangium wall. With the rapid growth of all the tissues the sporangium projects more and more above the surface of the sporophyll. The sporangium wall finally consists of three layers of cells, of which the inner one forms the "tapetum," whose cells are in contact with the sporogenous cells and contribute to the nourishment of the developing spores but remain permanently as part of the sporangium wall. The archesporial cells divide rapidly, finally separating to form the spore mother cells of the spore tetrads. The ripe sporangium opens by a transverse cleft.

In the more specialized species like *L. clavatum* the archesporium is more extensive and a radial section of the young sporangium shows about three primary archesporial cells instead of the single one of the *Selago* type. There is a corresponding increase in the number of spores in the ripe sporangium. The *Inundatum* type is intermediate in character between *L. Selago* and *L. clavatum*.

The gametophyte.—For many years the gametophyte of Lycopodium was practically unknown, and it was not until 1884 that the first comprehensive account was published by Treub. Treub's first paper described the gametophyte of L. cernuum, a common tropical species. This paper was followed by accounts of other species, especially the epiphytic L. phlegmaria. In 1898 a very important memoir on the gametophytes of several

European Lycopodiaceae was published by Bruchmann, who later supplemented this by an account of some other species and made extensive studies on the germination of the spores and the development of the gametophyte. These studies of Treub and Bruchmann have been followed by some later ones, including accounts of some American species by Spessard and especially the work of Holloway on several New Zealand species. From these investigations it is clear that the structure of the gametophytes in Lycopodium shows such extraordinary differences that it is evident the "genus" Lycopodium can hardly be considered the equivalent of the term genus as generally understood. In the majority of species examined the gametophytes are subterranean and destitute of chlorophyll; but exceptions are L. cernuum and a few related species.

Lycopodium cernuum is common in all of the warmer parts of the world. The upright shoots, often four or five feet high, form dense thickets and when they grow at the top of banks it is not difficult to find the young prothallia on the slope below them. The prothallia are inconspicuous—as a rule only one or two millimeters in diameter—but often fairly abundant. The gametophyte has a short cylindrical base, often buried in the ground, and bears at the top a tuft of irregular, green, leaf-like lobes.

According to Treub the germinating spores develop chlorophyll before the first cell division occurs, and within a few weeks there is formed an oval cell mass showing definite apical growth. This preliminary stage Treub calls the primary tubercle, from which is developed the cylindrical body bearing the lobes surrounding the apex of the older gametophyte, which thus shows distinct radial symmetry. A similar condition was found by Goebel in *L. inundatum*. In *L. cernuum* the gametangia are formed at the base of the lobes.

Bruchmann studied the germination of the spores and the development of the gametophyte in several of the species with subterranean prothallia and found that the spores required a very long time before germination began. In L. Selago the first signs of germination were first observed only after three to five years and in L. clavatum even longer. In L. Selago the first gametangia were found after six years, and twelve to fifteen years elapsed before mature gametangia were developed in L. clavatum. In these species a long period of rest intervenes between the primary tubercle stage and the adult condition. The early growth is at the expense of material contained in the ripe spores, since there is no chlorophyll and the development proceeds underground. After the food supply in the spore is exhausted, the future development is dependent on a symbiotic association between the young gametophyte and a fungus which enters the cells of the primary tubercle and establishes itself as an "endophytic mycorrhiza" like that found in the Psilotaceae.

The simplest form of subterranean gametophyte is found in L. Selago. The primary tubercle has a definite two-sidede apical cell and the infection with the endophyte occurs when the tubercle is composed of only a few cells. As the gametophyte grows it becomes a pear-shaped and finally a cylindrical body, not unlike the prothallium of Tmesipteris. Sometimes when growing near the surface of the ground the apex emerges and chlorophyll is formed. The green prothallia are much less elongated than the permanently subterranean ones. The apex of the gametophyte bears numerous gametangia interspersed with slender filaments (paraphyses). The

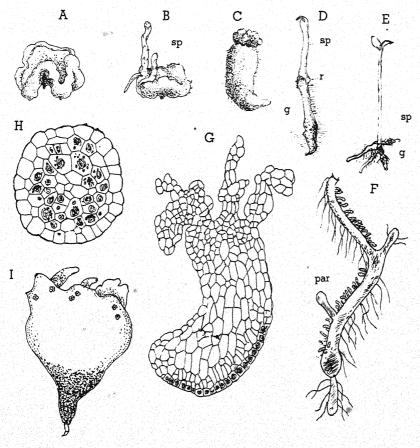


Fig. 124.—Gametophytes of Lycopodium. A, L. clavatum; B, L. annotinum; sp., young sporophyte; C, L. complanatum; D, L. Selago; g, gametophyte; sp., young sporophyte; r, primary root; E, L. Billardieri var. gracile; sp., young sporophyte; F, part of gametophyte of L. Billardieri, more enlarged; par, paraphyses; G, L. cernuum, section of young gametophyte of L. Billardieri, showing distribution of mycorrhiza; I, young gametophyte of L. ramulosum (A-D, after Bruchmann; E-I, after Holloway).

elongated subterranean prothallia in their later stages show a bilateral symmetry. The apex is covered with a layer of meristem-tissue which develops gametangia only on one side, while, on the other, rhizoids are formed.

The antheridia develop in acropetal succession and, later, archegonia arise in the same way. With the fertilization of the archegonium and the formation of an embryo the apical growth of the gametophyte stops.

Much like the subterranean gametophyte of L. Selago is that of L. phlegmaria, an epiphytic species, first investigated by Treub. Holloway has given a very full account of a similar species from New Zealand, viz., L. Billardieri. In these species the gametophyte consists of an irregularly shaped central body from which extend slender cylindrical branches, in structure much like the simple elongated prothallum of L. Selago. The gametangia are also much the same and are also associated with similar paraphyses. In L. phlegmaria Treub found that the prothallia were sometimes propagated by special buds, or gemmae. L. lucidulum, evidently related to L. Selago, has been shown by Spessard to have a very similar gametophyte.

The gametophyte of the common club moss, Lycopodium clavatum, represents a much more specialized type which is found in several other species. Bruchmann has described in great detail the development of the gametophyte from the germinating spore to maturity, a period of several years. He recognized three stages in this development.

The first stage extends from the germination of the spore to the completion of the primary tubercle, which, however, Bruchmann states develops in *L. clavatum* directly into the definitive gametophyte. As in *L. Selago*, this early stage has a definite two-sided apical cell and very soon is infected by the mycorrhizal fungus. The single apical cell is soon replaced by a group of initial cells, and later there is developed a condition much like that in the apical meristem of the stem-apex of the sporophyte.

The growth of the young gametophyte is very slow, but gradually the second phase is developed. The gametophyte now is a pear-shaped body whose upper surface consists of a layer of meristem tissue. At this stage there is a differentiation of the tissues into a central region composed of storage cells—containing starch and other reserve food. The endophytic fungus is restricted to the outer tissues, some three or four layers. In the older stages a single layer of radially elongated "palisade cells" is developed between the central region and the tissue occupied by the endophyte which is absent also from the apical meristem. Some of the superficial cells develop into rhizoids; sometimes there is a new infection of the mycorrhiza through these rhizoids, and through these the endophyte may also escape to the exterior.

In the third or final stage the apex becomes much broader and in shape the prothallium recalls a small cup-fungus (Peziza). The central part of the disc becomes elevated, forming a protuberance upon which are borne the gametangia. The antheridia develop first and later the archegonia. In the older prothallia the growth of the margin of the disc is very unequal, resulting in irregular folds and convolutions. The prothallium of L. volubile, described by Holloway, is much like that of L. clavatum, but as in L. Selago the prothallium sometimes emerges above ground and develops chlorophyll.

Corresponding in general with the structure in *L. clavatum* is *L. complanatum*, whose gametophyte is the most highly developed of any of the species. The subterranean gametophyte consists of a basal conical body sharply marked off from a terminal tuft of lobes, suggesting the green lobes of *L. cernuum*. There is the same segregation of the central storage tissue and the cortical region occupied by the endophyte. The palisade layer is even better developed than in *L. clavatum*.

It is generally assumed that the green prothallia of *L. cernuum* and *L. inundatum* represent the most primitive condition, the subterranean condition being secondary. Whether or not this view is correct, the subterranean types like *L. Selago*, *L. lucidulum*, and *L. volubile* are, in a sense, intermediate between the "holophytic" green gametophytes and the strictly saprophytic types like *L. clavatum*.

Bruchmann points out that there is a certain degree of correlation between the gametophyte and the sporophyte, the simpler sporophytes like those in L. Selago having a simpler gametophyte than that of the more highly specialized species, like L. complanatum. He also notes the similarity in the early stages of all the forms, the differences appearing later in their development. In all of them the "primary tubercle" has a two-sided apical cell and the next stage is a conical body, the broad apex covered by a zone of meristem tissue, which in L. Selago is a single cell layer but in the more specialized forms is three to four cells in thickness. In the Selago-type the development is more rapid, but the tissues are less specialized and a relatively larger region is occupied by the endophyte. L. complanatum shows the most highly differentiated gametophyte known among the pteridophytes. There is a sharply marked line between the vegetative and generative regions, and the former shows a very definite arrangement of the tissues. The endophyte is restricted to a very definite cortical zone, and it is evident from the abundant development of starch in the central region that the symbiotic relation between host and endophyte is effective.

Gametangia.—In all the species the gametophyte is normally monoecious, but the antheridia usually develop first. The antheridium in all the species of Lycopodium examined is more like that of the eusporangiate

ferns and Equisetineae in its structure than like the Psilotaceae; but the spermatozoids in the Lycopodineae differ from all the other pteridophytes in being biciliate like those of the bryophytes.

The antheridium originates from a superficial cell which divides by a transverse wall into an inner and other cell and the latter by further divisions forms the mass of spermatocytes. The cover cell divides by a series of intersecting walls, the last division resulting in a triangular operculum marking the point of exit of the spermatozoids. The antheridium, unlike that of the Psilotaceae, projects but little above the surface of the gametophyte. The number of spermatocytes varies a good deal in the different species and may be very considerable. In a single section of the antheridium in L. phlegmaria about two hundred spermatocytes are visible.

The development of the spermatozoid has not been followed in detail; but Bruchmann has studied carefully the free spermatozoids in *L. clavatum*. These are less specialized than those of other pteridophytes, the nucleus being little modified and not forming the major part of the sperma-

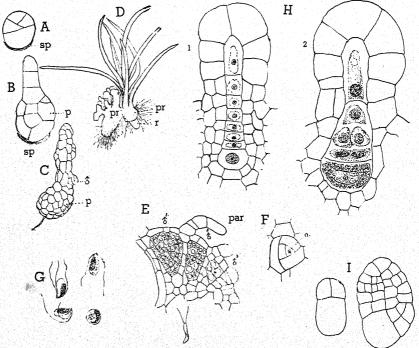


Fig. 125.—A, B, C, germination stages of Lycopodium cernuum; D, gametophyte of the same, with young sporophyte attached; E, F, antheridia of L. phlegmaria; F, surface view; C, spermatozoids of L. clavatum; H, archegonia; H, I, L. Selago; H, 2, L. phlegmaria; I, embryos of L. Selago (A-D, H, 2, after Treub; the others after Bruchmann).

tozoid. The latter is an oval cell, about twice as long as wide, the anterior end somewhat pointed and bearing two long flagella. The nucleus lies on one side of the cell, whose cytoplasm thus forms the greater part of the spermatozoid. It rather suggests the male gametes of some of the algae.

Spessard figures late stages of the spermatozoid in *L. lucidulum*, showing an elongated and curved nucleus much like that in many bryophytes. Treub's figures of *L. phlegmaria* show a similar condition and the free spermatozoid is elongated and somewhat twisted but is relatively thicker than in any of the Hepaticae or mosses.

The first division in the archegonium is like that in the antheridium. From the outer cell the neck is formed, while from the inner one the canal cells and egg are developed. The outer cell divides into equal quadrants from which the four rows of neck cells are formed. There is a good deal of difference in the length of the neck and the number of canal cells. Treub's figures of the archegonium of L. cernuum show a short neck and not more than two or three neck canal cells. Bruchmann's figures of L. Selago show about seven canal cells, while Miss Lyon found in L. complanatum as many as sixteen; and sometimes the canal cells were doubled, a condition also reported by Treub for L. phlegmaria. A still more notable variation was found by Spessard in L. obscurum, where bisexual gametangia were noted. These were archegonia in which the canal cells were partially replaced by spermatocytes, recalling the similar condition which has been found in some mosses.

The archegonium in *L. complanatum* as regards the number of canal cells has no counterpart elsewhere among the pteridophytes and is comparable in this respect to the true mosses. There may be also in some cases five instead of four rows of neck cells, also suggestive of the bryophyte archegonium.

The endophyte.—The relationships of the endophytic fungus invariably present in the gametophyte are still uncertain. The fungus lives in the humus soil in which the gametophyte is found and infects the gametophyte at a very early stage, as already noted. There may be also a more or less evident connection between the endophyte and the free-growing fungus outside. According to Bruchmann there are special cells at the base of the rhizoids whose function is to facilitate the entrance of the fungus-hyphae.

In the green prothallia, like L. cernuum, while the endophyte is present, it occupies a very much smaller portion of the tissue. In the simpler subterranean type, e.g., L. Selago, the endophyte has a less definite distribution than in the more specialized forms like L. clavatum and L. complanatum, where only a very definite cortical zone, all of whose cells are filled with a skein of fine hyphae, is thus invaded. The fungus is quite absent from the meristematic apical region and the central storage tissue. The young

cortical cells as they develop are invaded by the fungus, which bores through the cell wall and establishes itself. The granular contents of the host cell is evidently appropriated by the endophyte, but the cell is not killed and the nucleus remains perfectly normal.

According to Treub and Bruchmann, the hyphae, which are very slender, have no cross walls and the organism is referred to the Phycomycetes, a group of fungi which has a good many parasites on the higher plants—e.g., Phytophthora infestans, the potato blight. As no certain reproductive organs have been found, aside from spherical enlargements (sphaeromes) of the hyphae, whose nature is not clear, it cannot be assigned to any known genus. It has been compared to Pythium, a parasitic genus; but this is only tentative. In a recent paper, Spessard has described the endophytes in two species, L. obscurum and L. lucidulum. He claims that the hyphae are septate and therefore should not be assigned to the Phycomycetes. He suggests a possible relationship with Ascomycetes. However, some of his figures and descriptions indicate that some of them are not endophytes, but other fungi, perhaps growing on the dead tissue of the gametophyte.

There is no question that the association of the endophyte and host is a true symbiosis, both members benefiting equally.

The embryo.—The development of the embryo has been described for a number of species. Treub, Bruchmann, and Holloway have made the most important investigations on the embryogeny of Lycopodium. The species examined all agree in the earliest divisions of the zygote, but they show a good deal of difference in the later embryonic development.

The basal wall in the zygote is always transverse; and the primary cells, the one next the archegonium neck (epibasal), remains undivided, or divides once by a transverse wall, thus establishing the "suspensor," a feature characteristic of the Lycopodineae. The lower (hypobasal) cell alone develops into the embryo proper. In this embryonal cell the first division wall is somewhat oblique and divides the cell unequally. Each cell is divided again; and of the four quadrants thus formed the two next the suspensor form the foot of the embryo, the other two the primary leaf and the stem apex. The primary root is formed later from the same quadrant as the leaf.

In L. cernuum there is first developed an undifferentiated body, which Treub calls a "protocorm." From this are developed a number of elongated leaves, "protophylls," and later the definitive leafy shoot. The primary root, unlike the later ones, develops from the surface of the protocorm and not endogenously. Holloway has confirmed Treub's work on L. cernuum and has described a related species, L. laterale, in which the protocorm is extraordinarily developed, and forms a thickened rhizome, from which arise several protophylls and finally a typical leafy shoot. The proto-

corm is connected with the gametophyte by a definite foot—and this is true also of L. cernuum.

Corresponding with the late formation of the root and stem apex in L. cernuum is the delay in the formation of the vascular bundles, which Treub states are entirely absent from the protocorm and the first leaf (protophyll), which develops from the protocorm quite independently of the stem apex. Treub considers the protocorm as a primitive undifferentiated plant body which has disappeared in most existing pteridophytes, where it has been replaced by the definite leafy axis.

In L. phlegmaria and L. cernuum, which are tropical or subtropical species, the embryo probably continues its growth without interruption, the young sporophyte is soon established as an independent plant, and the first leaf is a functional green cotyledon. In the European species studied by Bruchmann, where the life of the gametophyte is so extraordinarily prolonged, this is true also of the young sporophyte, which sometimes does not appear above ground for several years after its development begins. The leaves of the subterranean shoots are rudimentary. Often several young sporophytes may be borne by a single gametophyte. Bruchmann found

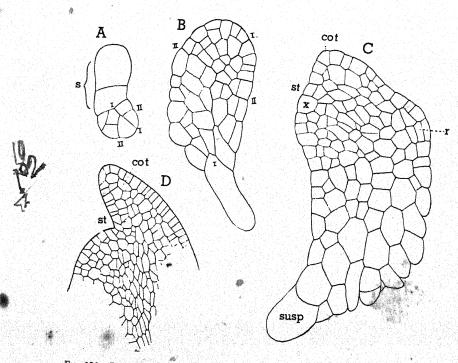


Fig. 126.—Development of the embryo of Lycopodium phlegmaria (after Treub).

that in *L. clavatum* and *L. annotinum* the first two leaves (cotyledons) were opposite. In *L. inundatum* the single cotyledon is a functional green leaf, as it is in *L. cernuum*.

The development of the central vascular cylinder, or stele, of the axis begins about the time the first root emerges. In L. Selago, where the young sporophyte arising from the subterranean gametophyte has a very elongated hypocotyl, the vascular bundle is monarch, i.e., has a single strand of xylem composed of a few small tracheids. After the first leaf is developed the bundle is diarch, as it is in the hypocotyl of L. clavatum. In the latter, four or five protoxylems develop as the shoot grows.

CLASSIFICATION OF THE LYCOPODIACEAE

Evidently related to Lycopodium is Phylloglossum Drummondii, a monotypic species found in New Zealand and Australia. The plant grows each season from a small tuber, or protocorm, which has been compared with that of the embryo of Lycopodium cernuum. From this protocorm several slender leaves are developed, much like the protophylls of the young sporophyte of L. cernuum. The protocorm also forms one or two roots which are exogenous like the primary root of L. cernuum.

In the mature plant the apex of the protocorm develops into an elongated axis bearing at the summit a short strobilus like that of Lycopodium. The anatomy of the sporophyte is of the Lycopodium-type, but the tissues are simpler. The gametophyte of Phylloglossum resembles that of Lycopodium cernuum.

Phylloglossum has sometimes been regarded as the most primitive of the pteridophytes; but Wernham, who has more recently investigated its structure, believes that it is a reduced, rather than a primitive, type.

All of the other Lycopodiaceae are usually united into the single genus Lycopodium. As we have already indicated, the differences shown by both gametophyte and sporophyte are so great that it does not seem logical to refer all the species to a single genus. Goebel recognizes five types based on the gametophyte; and there is a pretty well-marked parallelism between gametophyte and sporophyte. The five types, according to Goebel, are: (1) Selago; (2) Phlegmaria; (3) Cernuum; (4) Clavatum; and (5) Complanatum. Whether or not each of these groups should be raised to generic rank is a question.

Pritzel.

Pfitzer recognizes two subgenera, based upon the character and arrangement of the sporophylls. The first subgenus, *Urostachya*, includes those species in which there is not a definite strobilus. *Urostachya* is divided into two sections. The first is *Selago*, in which the sporophylls, except for the presence of the sporangium, are exactly like the sterile leaves. The stems here are sparingly branched, and the gametophyte is usually subter-

ranean but may be partially exposed and develop chlorophyll. L. Selago and L. lucidulum represent this section.

The second section, *Phlegmaria*, includes a number of characteristic epiphytic species from the tropical and south temperate regions. The type is *L. phlegmaria*, common in the eastern tropics. These species do not develop a definite strobilus, but the ends of the fertile branches fork repeatedly and are completely covered with the small sporophylls. The gametophyte is subterranean and is composed of a central body from which extend numerous slender branches. *L. pachystachyon* from Hawaii and *L. Billardierii* of New Zealand are other species of this group.

The second subgenus of Pfitzer, Rhopalostachya, includes three sections—Inundata, Cernua, and Clavata. Examples of the first are L. inundatum and L. alopeculoides. L. inundatum has a green gametophyte, much like that of L. cernuum. While there is a definite strobilus, the sporophylls are not very closely set, and are green and much like the sterile leaves.

The second section of Rhopalostachya is represented by L. cernuum, which resembles L. inundatum in the structure of the gametophyte but has a very much larger sporophyte. Lycopodium cernuum, which is common throughout much of the tropical and subtropical regions, has extensively creeping rhizomes, from which arise upright stems, sometimes five or six feet high, bearing many lateral dichotomous branches. At the tips of some of the branchlets are sessile strobili, composed of closely set, pointed sporophylls with fringed margins. The common "ground-pine" of the northeastern United States, L. obscurum (= dendroideum), which resemble a small L. cernuum, has been shown by Spessard to have a gametophyte of the clavatum type. In the last section of Rhopalostachya, Clavata, the fertile branches for some distance below the strobilus have the leaves greatly reduced in size, so that the strobilus appears to have an elongated pedicel. The sporophylls are small broad scales, closely set. The gametophyte reaches its most specialized form in this section of the genus. L. complanatum has the most highly differentiated gametophyte yet discovered among the pteridophytes.

These differences in the general morphology of the sporophyte, which are to a considerable extent correlated with the gametophytic structures, would seem to indicate the desirability of recognizing these five sections of the genus as distinct genera.

CHAPTER XI

LYCOPODINEAE: SELAGINELLACEAE; FOSSIL LYCOPODS

The Selaginellaceae, the second family of the living Lycopodineae, are at once distinguished from the Lycopodiaceae by their pronounced heterospory. On this basis the two families may be regarded as representing two orders, Selaginellales and Lycopodiales. Another character which distinguishes them is a peculiar appendage of the leaf, the "ligule," present in Selaginella but absent in Lycopodium; the two orders are sometimes named "Ligulatae" and "Eligulatae," but this distinction is less fundamental than the character of the spores.

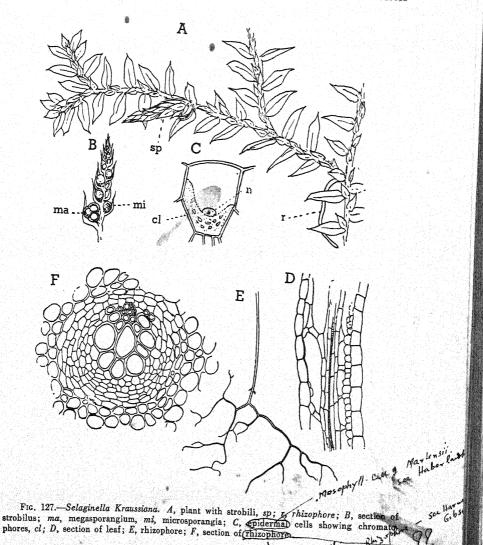
Included in the Ligulatae by many botanists is the peculiar family, Isoetaceae, in which a ligule occurs on the sporophylls. *Isoetes*, however, differs from *Selaginella* in several important structural characters which indicate that the Isoetaceae should not be included in the Lycopodineae.

The Selaginellaceae, with the single genus Selaginella, has about six hundred species, found in nearly all the warmer parts of the world. While they are predominantly inhabitants of the moister regions and reach their greatest developments in the tropical rain-forests, there are some species growing in arid regions, or on exposed rocks, where for much of the time they are completely dried up. Examples of these are S. rupestris, of the Eastern United States, and S. Bigelovii and S. lepidophylla of the Southwest. The latter is the "resurrection plant" of Texas and Arizona.

Selaginella includes a large majority of the Lycopodineae. In general structure the sporophyte of Selaginella resembles Lycopodium. The leaves may be all alike and placed spirally on the axis, or the shoot may be dorsi-ventral and the leaves arranged in four rows—two large and two small—on the dorsal side. Based on this difference in the leaf arrangement, the genus has been divided into two main divisions to which various names have been given. Hieronymus, in his elaborate treatment of Selaginella in the Natürliche Pflanzenfamilien, regards these divisions as subgenera, Homoeophyllum and Heterophyllum. In the tropical rainforests many species, mostly of the heterophyllous type, grow in profusion, most commonly on the ground, fallen logs, etc.; sometimes they are epiphytes. A few species, e.g., S. apus and S. ludoviciana of the Eastern and Gulf states and S. Douglasii of northern California and Oregon, are

heterophyllous. In the latter region occurs also the epiphytic S. oregana. Several species, e.g., S. Kraussiana, are common greenhouse plants.

The homoeophyllous species often have creeping stems attached by dichotomous roots, but there may be a definite rhizome from which upright shoots are developed. The small, crowded, lanceolate leaves are placed equally about the stem and are all alike. In the heterophyllous species the leaves are less crowded and arranged in four series on the upper side of the dorsi-ventral shoot. The leaves of the two inner series



are much smaller than the outer ones. In many of the heterophyllous species the roots are not developed directly from the main axis, but there are formed special leafless shoots—"rhizophores"—which develop from the apex a number of dichotomously branched roots. Each leaf has a median vascular bundle like the leaf of *Lycopodium*.

The strobilus is usually less conspicuous than in most species of Lycopodium; and in some of the homoeophyllous species, as in Lycopodium Selago, the sporophylls differ but little from the sterile leaves. The sporophylls are usually in four very regular series. In the heterophyllous species, the strobilus may replace a lateral branch and may have a more or less evident dorsi-ventral character.

Heterospory is found in all species of Selaginella, but a good deal of difference is shown in the arrangement on the strobilus of the mega- and microsporangia. For example, in S. Kraussiana the lowest (oldest) sporophyll alone bears a megasporangium, all the others being microsporangial; and in S. rupestris several of the lower sporophylls produce megasporangia. In S. atroviridis the cones are exclusively megasporangiate or microsporangiate.

Apical growth.—In nearly all species that have been examined the growth of the shoot is from a definite apical cell, thus resembling the Psilotineae rather than Lycopodium. However, there are exceptions, and

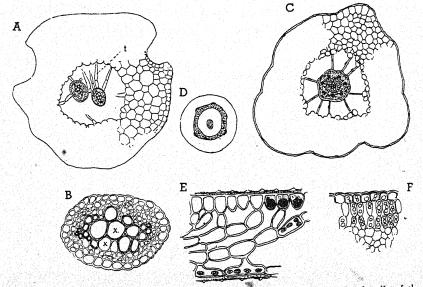


Fig. 128.—A, cross section of stem of Selaginella Kraussiana; B, vascular bundle of the stem; C, cross section of stem in S. spinosa; D, similar section in S. Lyallii; E, section of leaf in S. helvetica; F, similar section in S. Lyallii (C, F, after Harvey-Gibson).

Bruchmann found that in S. Lyallii, as in Lycopodium, there was a group of similar initial cells.

The conical apex of the shoot in S. Kraussiana shows a definite apical cell. The branches arise near the stem apex but are really lateral organs, the stem apex not being directly involved. The apical cell of the branch is formed independently, but the growth of the branch keeps pace with that of the main shoot and the effect is that of a true dichotomy. The leaves are formed in rapid succession. They have no single apical cell, and the early growth is due to the activity of a row of marginal initials.

Below the apex of the stem the central tissue becomes differentiated into an axial cylinder, which soon is separated from the cortifical region by a conspicuous lacuna, recalling the formation of the columella in many mosses. The axial cylinder remains in contact with the cortex by means of "trabeculae," elongated cells, which extend from the endodermis which encloses the central stele to the cortex. These trabeculae which seem to

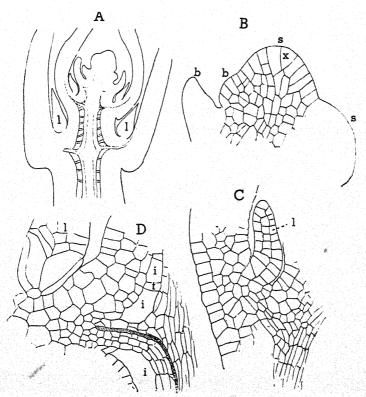


Fig. 129.—Selaginella Kraussiana. A, B, longitudinal sections of stem apex; b', young leaf; C, D, base of older leaves; l, ligule; i, lacunae.

originate from the endodermis are therefore considered to belong really to the cortical region.

In the majority of species this central cylinder becomes a single stele or vascular bundle; but sometimes, e.g., S. Kraussiana, the stem is bistelic, and in some others, e.g., S. laevigata, it is polystelic, with sometimes as many as a dozen separate steles. However, in all the species that have been examined the prostrate rhizome has a single stele which in the polystelic species gradually passes over into the separate steles of the upright shoot.

In the dorsi-ventral shoots where there is a single stele it is strongly flattened or ribbon-like. In his very complete study of the anatomy of Selaginella, Harvey-Gibson has given a detailed account of the different

types of the stelar structures.

In the more delicate species, like S. Kraussiana, the cortex is composed of thin-walled green parenchyma, but in the xerophytic species like S. rupestris, or S. lepidophylla the cortex is for the most part made up of sclerenchyma cells with thick, deeply pitted walls, and the lacuna between the cortex and the axial stele is almost entirely obliterated, and the outer cortex in most species with rigid stems has a greater or lesser amount of hypodermal sclerenchyma.

A section of the steles in S. Kraussiana shows within the endodermis a pericycle of a single layer of cells, within which is the phloem completely surrounding the axial mass of xylem. The vascular bundle is therefore "concentric" in structure. At the foci of the elliptical section are two groups of small spiral and annular tracheids—the protoxylems—and between is the mass of econdary wood, the "metaxylem," composed of large scalariform tracheids. The phloem contains sieve tubes, with thin walls, having numerous lateral sieve plates, which, however, are not very well developed.

The leaf.—The leaves are much like those of Lycopodium; they are thin and delicate in texture in most species, but in such xerophytic forms as S. rupestris and S. bigelovii they are relatively thick and rigid. In the heterophyllous species the leaves may be quite symmetrical or the two halves may be unequal in size. The epidermis of the two surfaces may be alike or different. Usually, but not always, stomata are confined to the abaxial surface. The mesophyll is usually composed of similar cells which are more or less elongated with intercellular spaces, which often are much enlarged, so that the elongated mesophyll cells form an open network with large intercellular spaces. Sometimes, e.g., in S. Lyallii, there is a well-developed palisade parenchyma below the upper epidermis.

The vascular bundle of the leaf is concentric, and the leaf traces join the stele of the shoot. Both xylem and phloem are simpler than those of the stem bundle, and a definite endodermis cannot be demonstrated. The ligule appears at a very early stage of the leaf development. When full grown it is a flattened scale, which is lanceolate in outline in some species, fan-shaped or broadly wedge-shaped in others. When fully developed it has a basal portion, the "glossopodium," composed of large elongated cells which are surrounded by a sheath of cells continuous with the epidermis of the leaf.

The chloroplasts of Selaginella are peculiar among the vascular plants and recall those of the Anthocerotes. In the epidermal cells of the leaf there may be but a single large chloroplast or a division into two; but in the mesophyll cells and in the cortical cells of the stem there are several, which, however, are connected with each other. An aggregation of starch grains in the center of the plastid, sometimes surrounding a central body, possibly may be compared with a pyrenoid. Haberlandt found a single plastid in the meristematic cells of the stem apex. This single condition was retained in the epidermal cells of the leaf, and where there was more than one in a cell they were evidently the result of a division of a primary plastid.

Megaceros, one of the Anthocerotaceae, offers a somewhat analogous case. The retention in Selaginella of what is probably a very primitive type of chloroplast is interesting.

The root.—The roots may develop directly from the ventral side of the rhizome but in many of the heterophyllous species like S. Kraussiana they are borne at the apex of a "rhizophore." This is usually regarded as a leafless stem, since the anatomy corresponds with that of the leafy shoot. The roots originate from hypodermal cells at the end of the rhizophore but do not involve its growing point. According to Sadebeck, before the roots are formed the apical cell of the rhizophore is replaced by a group of initial cells. The apical cell of the young root is formed independently from a hypodermal cell, which soon develops the characteristic tetrahedral form of the root apical cell. The young root soon emerges and later undergoes repeated dichotomy. The growth of the root from the apical cell is much like that of the stem apex; but from the outer face of the apical cell segments are formed which contribute to the growth of a root cap.

The vascular cylinder of the root is "monarch," i.e., there is a single protoxylem. The phloem surrounds the xylem as in the leaf bundle; but, according to Harvey-Gibson, sieve tubes are absent from the phloem in the region opposite the protoxylem.

The sporangium.—The sporangium of Selaginella in its early development is very much like that of Lycopodium. Each sporophyll has a sporangium in its axil; the sporangium is generally developed from the surface of the shoot, above the insertion of the sporophyll; but Bower states that

sometimes the sporangium forms very close to the leaf base. In radial section the appearance is much like that of Lycopodium. In S. Kraussiana such a section shows an axial row of cells, of which the central one belongs to the archesporium. Comparison with other species that have been studied, especially by Bower, makes it likely that the single archesporial cell seen in the radial section is one of a transverse row of similar cells, as in Lycopodium Selago. In S. Martensii the radial section shows two archesporial cells, a condition also shown by some species of Lycopodium.

Like Lycopodium the wall of the sporangium has two layers of cells, within which is the tapetum, whose cells remain intact until the spores are nearly or quite ripe. Bower states that the tapetum in Selaginella is derived from the archesporial tissue, and is not formed from the parietal region as it is in Lycopodium. In the later stages of the sporangium in Selaginella the tapetal cells are papillate in form and suggest an epithelium. They are in close contact with the developing spores and evidently intimately associated with their growth.

The sporangia are all alike in their early development and this con-

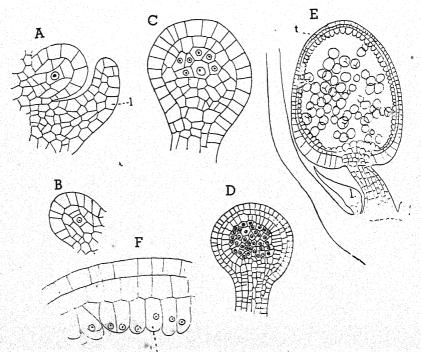


Fig. 130.—A-D, development of the sporangium in Selaginella Kraussiana; E, microsporangium; F, wall of young megasporangium; t, tapetum.

tinues up to the formation of the spore mother cells. In the microsporangia all of these undergo the normal tetrad division; but in the megasporangium usually only one mother cell divides, the others later becoming broken down and contributing to the growth of the single tetrad of megaspores. These become greatly enlarged and finally completely fill the sporangium, which is much larger than the microsporangia. The cells of the sporangium wall and tapetum remain active up to the time the spores are ripe, the tapetum being in close contact with the thick outer coat of the spore membrane, and undoubtedly are intimately concerned with the transport of food to the developing spore and the young gametophyte within it. The growing megaspore for a long time contains very little cytoplasm, and the growth of the thick spore membrane is due to the activity of the tapetum. Unlike the megaspores of the other heterosporous pteridophytes, which when ripe are uninucleate, the ripe megaspore of Selaginella contains the young gametophyte, which sometimes has already formed young archegonia. The microspores also begin germination while still within the sporangium. The first division results in the formation of a small "prothallial" cell and a large antheridial one. The first division in the antheridium is a median vertical wall.

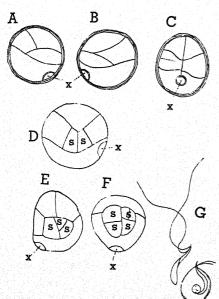


Fig. 131.—Development of the male gametophyte of Selaginella. A-D, S. Kraussiana; E, F, S. stolonijer; s, spermatozoids of S. cuspidata (all figures after Belajeff).

A recent study of the male gametophyte in S. Kraussiana by R. A. Slagg indicates that each of the two primary cells of the antheridium is divided by a nearly transverse wall so that the antheridium is divided into somewhat uneven quadrants. In each upper quadrant, by a series of divisions, two central cells are formed, surrounded by three peripheral ones. Slagg states that the "microgametophyte" when shed consists usually of thirteen cells-one prothallial, eight "jacket" cells, and four primary spermatogenous cells. From the latter, a total of 256 spermatozoids are produced. According to Belajeff there may be only one central cell in each half of the antheridium.

With the multiplication of cells in the primary spermatogenic cells the four groups of spermatocytes become fused into a single globular mass, which floats free in the cavity of the antheridium, owing to the disintegration of the surrounding cells. From each spermatopartie a single biciliate spermatozoid is set free.

The female gametophyte.—The growth of the female gametophyte has much in common with that of some of the primitive seed plants. Like the latter, the development of the gametophyte begins while the megaspore is still within the sporangium, the process beginning long before the spores are full grown. The materials for the growth of the young gametophyte are not stored food, as in other heterosporous pteridophytes, but are supplied through the activity of the parietal and tapetal cells. The gametophyte is thus, in a sense, parasitic upon tissues belonging to the sporophyte.

In the earliest stages the megaspore contains very little cytoplasm which forms a very thin film lining the cell wall. The wall of the young megaspore is composed of three coats, the outer one, the "exospore," and a

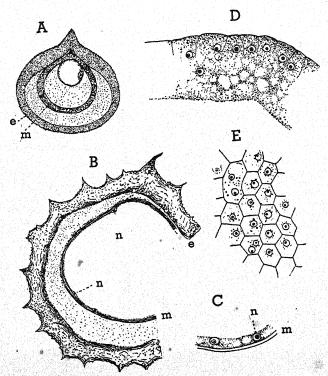


Fig. 132.—A, young megaspore of Selaginella helvetica, showing the vesicular protoplast and nucleus, and the two spore membranes; $B^{\pm}E$, early stages in the development of the female gametophyte of S. Kraussiana; m, mesospore; n, nuclei (A, after Fitting).

middle one, the "mesospore," being much thickened. The former grows much faster than the mesospore which becomes separated from it, except at one point. The inner coat, the endospore, is very thin and is in close contact with the mesospore. The cytoplasm forms a very thin film, enclosing the single minute nucleus. With the rapid growth of the spore membranes, due to the activity of the tapetal cells, the cytoplasmic film of the spore becomes detached and appears as a small vesicle in contact with the inner spore membrane. This cytoplasmic vesicle, which can be clearly seen in the young spore, was long mistaken for the nucleus of the spore. Fitting first demonstrated the real nature of the cytoplasmic vesicle. which has been verified by later investigators. The nucleus is very minute and soon divides, until the cytoplasmic film which increases in size and thickness contains many free nuclei. Finally the cytoplasm comes into close contact with the inner spore membrane (endospore). The growth of the cytoplasmic layer is more active at the apex of the spore, where the nuclei are more numerous, than in the basal area; and with the rapid increase in the cytoplasm it encroaches upon the large central vacuole, which finally is completely obliterated.

Cell formation begins in the apical region. In S. Kraussiana, at this time, the numerous nuclei in the apical region are in a single layer. Simultaneously delicate cell walls form between the nuclei, resulting in a layer of "areoles," each usually containing a single nucleus. The areoles are open below and their formation is very much like the early endosperm formation in many seed plants.

Cell formation for a time is confined to the apical region, which is occupied by a lens-shaped cellular body, while the cytoplasm of the rest of the spore contains only free nuclei. The inner face of the apical cellular prothallium body may have the cell walls much thickened, forming a conspicuous diaphragm between the apical body, which may be called the generative region, and the spore cavity, which we may call the vegetative region. Finally cell walls appear in the latter, and ultimately the whole spore is filled with cellular tissue. In some species, e.g., S. apus, there is no diaphragm developed and there is no definite line between the apical (primary) and basal (secondary) tissue of the gametophyte.

In S. Kraussiana the first archegonium is formed about the time the spores are shed. Later, others are developed. They differ much from those of Lycopodium in the greatly reduced structure of the neck. Each of the four outer rows has but two cells, and there is only a single neck canal cell.

The formation of the cellular tissue below the diaphragm begins, in S. Kraussiana, about the time the first archegonium can be seen. These secondary cells of the gametophyte are much larger and more irregular

in form than those of the generative region, and often are multinucleate. These cells finally are filled with food materials—largely albuminous granules and oil.

The development of the gametophyte is much more advanced in some species than in others at the time the spores are shed. In S. Kraussiana the first archegonium is nearly mature and the apex of the gametophyte soon emerges from the spore. Sometimes the free portion of the gametophyte develops numerous rhizoids. In S. Galeotti, described by Bruchmann, the numerous rhizoids are borne on conspicuous prominences, and probably by these nutriment may be conveyed to the developing embryo.

Miss Lyon found that in S. apus and S. rupestris the development of the gametophyte was completed before the spores were shed and that fertilization might take place while the spores were still within the sporangium

-a condition somewhat analagous to that in the seed plants.

The embryo.—Like Lycopodium the embryo of Selaginella has a suspensor. Most commonly the basal wall separates the suspensor from the body of the embryo; but there are several different types which have been described by Bruchmann, who has made a careful comparative study of several species. Among these, S. denticulata may serve as an illustration.

In S. denticulata the primary epibasal cell develops the suspensor, in

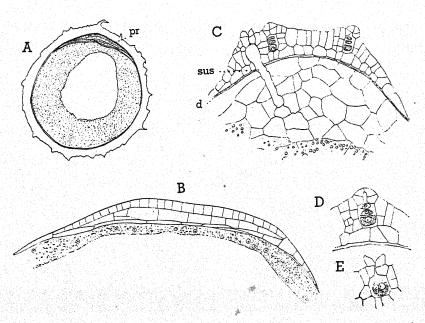


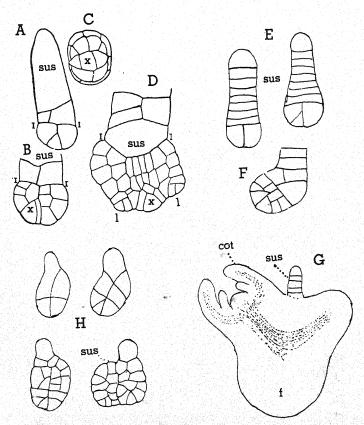
Fig. 133.—Older stages of the female gametophyte of S. Kraussiana. A, section of nearly ripe megaspore, with gametophyte.

which several cross walls are formed. In the hypobasal cell a vertical wall divides it into two nearly equal cells. In one of these an oblique wall marks the position of the stem apex, where a definite apical cell is soon established. The basal cell of the suspensor increases in size and on the side opposite to the stem apex divides into several cells, this growth causing the basal wall to assume an almost vertical position, so that the axis of the young shoot lies at right angles to that of the suspensor.

From the second of the two primary hypobasal cells the first leaf, or cotyledon, develops while from the first segment of the apical cell of the stem a second cotyledon is formed; thus the young sporophyte is "dicoty-

ledonous."

The apical cell of the stem is usually tetrahedral; but there is less regularity in the succession of the segments than in many other cases. The



Fic. 134.—Embryogeny in Selaginella. A-D, S. Martensii; E-G, S. denticulata; H, S. rubricaulis; sus, suspensor (A-D, after Pfeffer; E-H, after Bruchmann).

cotyledons do not show a definite apical growth, but the growth is due mainly to the active growth of marginal initials.

The hypobasal region in S. denticulata gives rise only to the stem, the cotyledons, and the hypocotyl—the region between the cotyledons and the foot. The latter is formed from the basal cells of the suspensor, and is very large. From the upper part of the foot is formed a conical protuvery large, which is the primary rhizophore from which later the first roots develop.

As the embryo sporophyte grows, a central strand of narrow cells, "procambium," is formed in the axis of the young shoot, and in each cotyledon a similar strand develops which joins the stele of the shoot. Somewhat later the stele of the stem is continued into the young rhizophore.

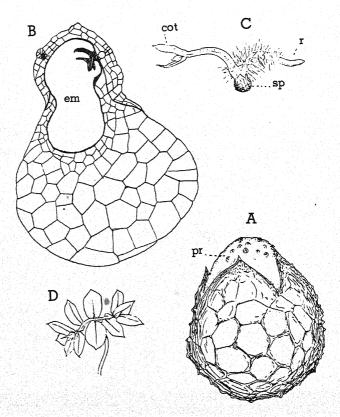


Fig. 135.—A, germinating megaspore of Selaginella Kraussiana; pr, the gametophyte; B, section of a large embryo enclosed in the gametophyte; C, young sporophyte attached to the megaspore; cot, cotyledons; r, root; D, young sporophyte showing dichotomy.

In S. Martensii the epibasal cell of the two-celled embryo develops only the suspensor, all of the organs of the embryo sporophyte being formed from the hypobasal cell. In another type, represented by S. Galeotta, the stem apex and both cotyledons are of epibasal origin, while the other organs-hypocotyl, foot, suspensor, and rhizophore-belong to the hypobasal region. In all of the forms the cotyledons, like the later leaves, have a ligule.

S. Kraussiana differs markedly in the first stage of development from most of the species that have been investigated. After fertilization the protoplast of the zygote contracts and a new cell wall is developed about it. It then divides into two cells. The two-celled embryo is thus enclosed in a membrane, which rapidly elongates and carries the two-celled embryo deep into the nutritive tissue below the generative apical region. No proper suspensor is developed, the tube containing the young embryo

taking its place.

As the young plant emerges from the spore there is a rapid elongation of the hypocotyl, which bears at its summit the pair of cotyledons with the stem apex between them. The rhizophore also emerges and bends downward, and the first root from its apex penetrates the ground. The foot remains within the spore; and the young plant might well be mistaken for a typical dicotyledonous seedling. The primary shoot may remain unbranched for some time, but it may at an early stage show a true dichotomy of the stem apex resulting in two equal diverging branches.

THE RELATIONSHIPS OF THE LYCOPODINEAE

The many close resemblances in structure indicate a real relationship between the Lycopodiaceae and the Selaginellaceae; but it is evident that the two families represent two distinct lines of development that have existed since the Paleozoic Age. How far back the presence or absence of the ligule is a fundamental difference is not certain, but the difference in the spore characters can be traced to the most ancient representatives.

Lycopodium-like types occur in the Devonian, and a connection of the Lepidophyta with the Psilophyta, through forms like Protolepidodendron,

is quite conceivable.

The simple stele of most species of Selaginella is probably a more primitive condition than the much more complex stele found in Lycopodium. The growth of the stem from a single apical cell in Selaginella, as it is in the Psilotales, suggests a more primitive condition than the multicellular apical meristem of Lycopodium.

The evolution of the plant body in the two families is along similar lines. In both, the simpler and probably older type is an upright radially symmetrical shoot with uniform leaves. The dorsi-ventral structure, with



heterophyllous leaves, found in most species of Selaginella and a few species of Lycopodium, is probably secondary. As might be expected, the oldest fossils resembling the Lycopodineae are homosporous, like Lycopodium, while the heterosporous Selaginella is presumably a more recent development.

FOSSIL LYCOPSIDA

Among the Paleozoic fossils are numerous impressions of plants which superficially, at least, closely resemble the existing genera, Lycopodium and Selaginella, and have been named Lycopodites and Selaginellites according as they are homosporous or heterosporous. The anatomy of these is very imperfectly known; but the close general resemblance makes it likely that these fossils are really related to the living forms, which would thus be the little changed descendants of Paleozoic ancestors. Lycopodites occurs from the late Devonian through the Paleozoic. Selaginellites is not known back of the Carboniferous.

Probably the oldest fossil that can be assigned definitely to the Lycopsida is *Protolepidodendron*, from the middle Devonian. *P. Scharyanum* has been investigated recently by Kräusel and Weyland. This remarkable fossil was known only from impressions; but these investigations show some further important details of structure which indicate that it has much in common with the Lycopodiales. It derives its name from the elongated, cushion-like areas marking the leaf bases and suggesting the characteristic leaf cushions in *Lepidodendron*.

The stem in Protolepidodendron has a central stele, with a solid core of xylem, which appears triangular in section. This is enclosed by a zone of phloem, and the stele is comparable to that of some of the living Lycopodineae. The triangular section of the xylem perhaps indicates the presence of three protoxylems. There seems to have been a prostrate rhizome from which were developed upright leafy shoots like those in many species of Lycopodium. The leaves on these upright shoots, however, were forked, thus differing from any of the existing Lycopods, recalling the phylloids of the Psilophyta, and suggesting the possibility of a derivation of the Lycopsida from the Psilophyta through forms like Protolepidodendron. The sporangia of the latter are borne on the adaxial surface of the sporophyll, as in Lycopodium; but the sporophyll is forked like the sterile leaves. No ligule is developed. Protolepidodendron primaevum, occurring in late Devonian rocks in western New York, had an upright stem, probably twenty feet or more in height, forking at the summit, the branches bearing leaves resembling those of Lycopodium.

From the later Devonian through the Carboniferous the Lycopsida play a leading role in the vegetation, especially in the Coal Measures. Some of these, especially Lepidodendron and Sigillaria, were sometimes tall trees comparable in size to many living conifers. In some species of Lepidodendron the massive tapering trunk reached a length of 30 meters. The broad base of the trunk was supported by thick, dichotomously branched, root-like structures, which were of the nature of a rhizome rather than true roots. These structures bore numerous relatively slender roots, which finally fell off, leaving definite circular scars. These rhizomes, before they were recognized as belonging to Lepidodendron, were called Stigmaria.

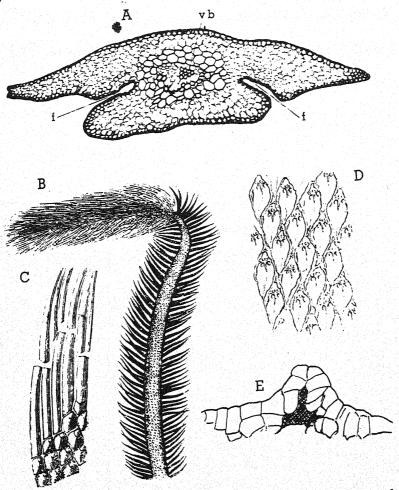


Fig. 136.—Fossil Lycopodineae. A, section of leaf of Lepidodendron Hickii; vb, vascular bundle; B, L. Ophiurus; C, leaves of L. Ophiurus; D, stem surface of L. Veltheinianum, showing leaf scars; E, archegonium of L. Veltheinianum (A, D, after Scott; B, C, from Scott, after Zeiller; E, after Gordon).

The tall trunk of Lepidodendron divided at the summit into a crown of many leafy branches. The branching was dichotomous; but sometimes the dichotomy was unequal and the branches formed a sympodium. Lepidodendron, except for its great size, must have resembled in habit Lycopodium cernuum or the ground-pine, L. obscurum.

Except for the oldest part of the trunk, its surface was marked by very characteristic, diamond-shaped leaf cushions, each with a central scar where the leaf had been attached. This is very much like the leaf cushions found in many conifers. Lateral branching is rare.

The leaves of Lepidodendron were confined to the younger branches and in general structure were like those of the living Lycopods, having a single median vascular bundle. They were larger, however, sometimes 15 centimeters long, and in some species were very narrow—recalling the "needles" of the conifers. The leaves have a ligule, thus resembling Selaginella rather than Lycopodium.

The sporangia were borne singly on the sporophylls, which formed a cone or strobilus at the top of a branch, thus resembling many species of Lycopodium. These cones were structurally much like those of the living Lycopodineae; the cones are usually described under the name Lepidostrobus. There are both homosporous and heterosporous forms. The megasporangium, according to Hirmer, usually contains eight to sixteen megaspores, but sometimes only four, as in Selaginella. The free spores often occur in immense numbers in coal seams and the accompanying shales.

Anatomy.—The tissues of Lepidodendron have sometimes been very perfectly preserved. Sections of the stem in some species resemble the structure in coniferous trees. There is a massive cylinder or stele with a central pith surrounded by a cylinder of wood which may show a development of secondary wood due to the formation of a meristematic tissue, the cambium, between the xylem and the phloem. The woody tissue is less developed than in the conifers, and outside the stele is a very thick cortex in which is also present a meristematic tissue, phellogen, to which the increase in thickness of the stem is mainly due. The mechanical, or strengthening tissue, instead of being the wood as it is in the conifers, like Lycopodium, is mainly cortical tissue. In some species there is no pith and no secondary wood. Where a cambium is developed and secondary wood is formed, medullary rays may occur, and the stem structure is very much like that of a conifer; but no cases have been observed indicating seasonal growth rings such as are present in most conifers.

In their anatomical structure the leaves recall the "needles" of a pine or fir. The single vascular bundle is "collateral," and on the abaxial (lower) surface are two furrows containing numerous stomata.

The root.—Zimmermann suggests that the rhizome (Stigmaria) of Lepidodendron, like that of the Psilotales, might be regarded as a structure intermediate between a true stem and a root. This might also be applied to the rhizome of Lycopodium where the stelar structure is much like that of the roots of the modern seed plants. It is not likely, however, that this indicates any genetic relationship between the latter and the Lycopodineae.

The true roots arise from the stele of the rhizome and penetrate the cortical tissue, thus being strictly endogenous like those of the higher plants. The stele of the root is monarch, i.e., has but one protoxylem.

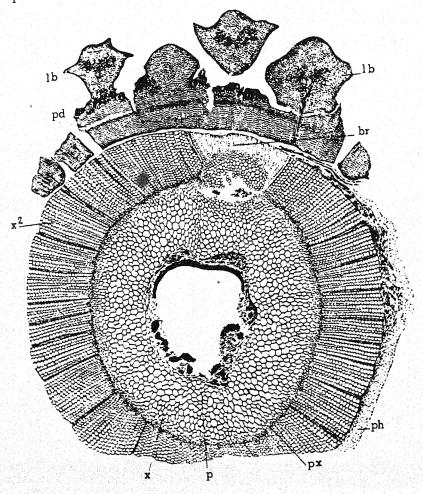


Fig. 137.—Cross section of a young stem of Lepidodendron brevifolium (after Scott).

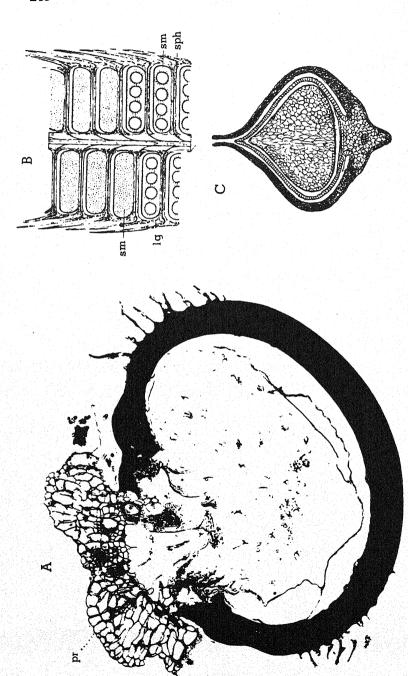


Fig. 138.—A, megaspore of Bothrodendron mundum, with gametophyte, pr; B, diagram showing section of the heterosporous strobilus of Lepidostrobus; sm, microspores; lg, megaspores; sph, sporophyll; C, seed of Lepidocarpon lomaxi, somewhat diagrammatic (A, after McLean; B, C, after Scott).

The sporangium.—The sporangia are elongated flattened bodies borne singly on the sporophyll. The latter consists of a horizontal narrow portion to which the sporangium is attached, and an outer broad lamina which bends upward and conceals the sporangium. One of the most perfectly preserved forms, Lepidostrobus Brownii, has been described in detail by Professor Bower. The cone was two inches in diameter, and in cross section showed a circle of about thirteen sporophylls. The sporophyll has the free apex, or lamina, turned up so as to protect the large sporangium. This covers the upper surface of the narrow horizontal portion of the sporophyll, to which it is attached by a narrow "flange" extending its whole length.

The wall of the sporangium is composed of several cell layers, the outermost having heavy cell walls. From the flange, which attaches the sporangium, an irregular ridge of sterile cells projects into the sporangium cavity; this sterile ridge has been compared by Bower to the "trabeculae" bands of sterile tissue in the sporangia of Isoetes. The spores in L. Brownii are all alike. It was probably homosporous; some other species, e.g., Lepidostrobus Veltheimianus, were heterosporous; and megaspores with the enclosed prothallium have been found.

ARCHAEOSIGILLARIA

In the upper Devonian of New York a very remarkable fossil, Archaeosigillaria primaeva, was discovered. This plant seems to combine, to some extent, the characters of Lepidodendron and Sigillaria, and perhaps represents an older archaic type from which the later more specialized forms have been derived.

Archaeosigillaria had an upright, apparently unbranched trunk; but, instead of the branched rhizome of Lepidodendron and Sigillaria, the base of the trunk had a swollen bulbous form, recalling the condition in Hornea. From this, bulbous base roots like those of Stigmaria were produced.

SIGILLARIA

Other characteristic Paleozoic genera are Sigillaria, Bothrodendron, and Lepidophlois. Of these the most conspicuous was Sigillaria, which, like Lepidodendron, included trees of considerable size. The trunk branched less freely than in Lepidodendron, and the leaf cushions were in regular vertical rows and were simpler in form. The leaves were crowded and longer than those of Lepidodendron, in one species being about a meter in length. The cones are not borne by the ordinary branches but were formed on special lateral branches developed from the upper part of the trunk. This is true of Bothrodendron also.

Sigillaria appears somewhat later than Lepidodendron, but is abundant in the later Carboniferous. All of these giant lycopods apparently became extinct before the end of the Paleozoic, and there is no satisfactory evidence that they have left any descendants. The living Lycopodineae probably are the little-changed descendants of forms like the late Devonian and Carboniferous Lycopodites. Bothrodendron is evidently related to Levidodendron and Sigillaria; but some of the species were much smaller and their leaf scars were less conspicuous. The stem structure is similar, but the slender twigs and small leaves recall Lycopodium or Selaginella. A petrified cone mentioned by Seward was only about ten millimeters in length—comparable in size to that of Selaginella, which it very much resembled in structure, the sporangium being erect, with a short pedicel, and globular in form. The megasporangia contained only four spores, like Selaginella; but there was no difference in size between the two sorts of sporangia. A most remarkable discovery was a petrified specimen of the megaspore of Bothrodendron mundum in which the prothallium was clearly shown connected with the megaspore. It resembled that of some species of Selaginella but was still more like the female gametophyte of the water-fern, Azolla. Bothrodendron occurs in the later Devonian and early Carboniferous.

It is known not only that some of the Paleozoic Lepidophyta had attained to heterospory but also that in some cases true seeds occur, although these are very different from those of any living seed plants. Some of these have been described under the name *Lepidocarpon*. These seeds are evidently a further development of the heterospory shown in some

other fossil lepidophytes and in the living Selaginella.

One of the best known of these is Lepidocarpon lomaxi. The seed differs from the usual megasporangium in being protected by a special envelope, the integument which extends above the apex of the sporangium and forms a narrow canal or "micropyle" through which possibly spermatozoids escaping from the germinating microspores may have entered and fertilized the archegonia. That archegonia were formed is known in some cases, but at present little is known about how fertilization was accomplished; and whether or not the embryo was developed while the seed was still attached to the parent plant is uncertain. Miadesmia is another fossil seed associated with the Lepidodendraceae.

A recent paper by W. C. Darrah describes a fossil referred to the living genus Selaginella. Megaspores with the young gametophyte were

present. This fossil was from the Upper Carboniferous.

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CHAPTER XII

EQUISETINEAE (ARTICULATAE)

The genus Equisetum, the sole survivor of an ancient race which has otherwise completely disappeared, is especially interesting to the botanist.

At present there are about twenty-five species, mostly restricted to the North Temperate Zone but with several tropical ones in the West Indies and South America, some reaching as far south as Chile. The North Temperate species are mostly common to North America and Eurasia. More than half of the species are found in the United States. A single species, E. debile, extends from India through the Malayan Archipelago to some of the Pacific islands. Two species, E. arvense and E. ramosissimum, occur in South Africa; but as these grow also in Mediterranean regions, it is probable that they were introduced from North Africa. None of these are known from Australia or New Zealand.

All of the species have a rhizome from which the upright aerial shoots develop. The thizome branches freely and sometimes, as with the common "horse-tail," E. arvense, the plant may become a troublesome weed. In size they range from E. scirpoides, whose slender shoots are only a few inches in length and one to one and one-half millimeter in thickness, to E. giganteum from the American tropics, which may be ten meters high but with a relatively slender stem which requires the support of the shrubs or trees among which it grows. Another tropical species, E. Schaffneri, is said to have a diameter of ten centimeters; but its hollow stem is much shorter than that of E. giganteum.

In spite of the great difference in size, the structure is very uniform. The stem is always composed of a regular succession of nodes bearing the leaves and branches and elongated internodes between them. The leaves are rudimentary and united into a sheath surrounding the node. These leaf sheaths have little or no chlorophyll and are mainly protective in function. The apex of the young shoot is completely enclosed in the closely set sheaths of the younger nodes. The chlorophyll is mainly restricted to the cortical tissue of the internodes.

The sporangia are borne on sporangiophores which surround the upper nodes of the fertile shoots. The internodes in this region are very short, so that the whorls of sporangiophores are close together and form a compact cone at the apex of the shoot. The genus has been divided into two sections: *Euequisetum*, in which new shoots are formed each season and

in which there may be special fertile shoots, e.g., E. arvense; and Hippochaete, where the shoots are perennial and strobilus is borne on unmodified shoots. E. hiemale, the common "scouring rush" and E. robustum are examples of Hippochaete. In E. arvense and E. maximum (= E. telmateia) the fertile shoots are unbranched and almost completely destitute of chlorophyll, collapsing after the spores are shed. Later the sterile shoots develop. These bear at the nodes whorls of slender green branches which contain most of the green tissue and are the photosynthetic organs. In E. sylvaticum secondary branching occurs.

In some of the species of Hippochaete, like E. hiemale, few or no

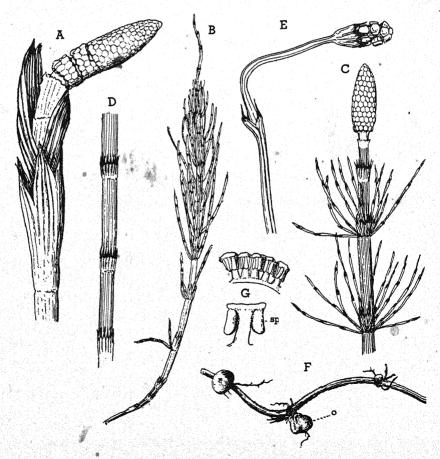


Fig. 139.—Equisetum. A, E. maximum, fertile shoot; B, sterile shoot of E. arvense; C, D, E. limosum; E, E. scirpoides; F, rhizome of E. arvense, showing tubers, o; G, sporangiophores and sporangia of E. maximum.

branches are developed; but in others, e.g., E. giganteum, a whorl of many branches, some of which may bear cones, are formed about the nodes.

The internodes have longitudinal furrows corresponding in number to the teeth of the foliar sheaths. The branches develop from the stem within the sheath but penetrate the base of the sheath and emerge outside. The superficial cells of the internodes have a heavy incrustation of silica, making the surface rough to the touch—hence the name, "scouring rush."

The nodes form solid diaphragms separating the hollow internodes. The latter have a large central cavity outside of which is a ring of vascular bundles corresponding to the longitudinal ridges on the surface of the internode. Alternating with the bundles are large lacunae in the cortex and in each bundle. Marking the position of the protoxylem is a small lacuna, the "carinal canal." The bundles are collateral and resemble those of some of the simpler monocotyledons. There are three groups of tracheary tissue, the one adjacent to the carinal canal and two lateral groups. The protoxylem elements have annular thickenings, the secondary (metaxylem) spiral as well as annular tracheids. The phloem is composed of thin-walled "cambiform" cells and sieve tubes.

In E. maximum, outside the ring of vascular bundles, is a common endodermis; but in some cases, e.g., E. limosum, each bundle has a separate endodermis. In some others, e.g., E. hiemale, there is a common endodermis like that in E. maximum and a similar one inside the ring of bundles. A limited secondary growth of the bundles has been found in the nodes of E. maximum.

The bundles alternate in position in successive internodes, owing to the alternation in the position of the leaves in successive nodes. The leaftrace divides in the node and joins the internodal bundle below the node, and each of the internodal bundles is made up of a union of the branches from two leaf traces. At the node the alternate bundles of successive internodes are connected by short branches which form a continuous ring of vascular tissue in the node.

Where the stem is unbranched, e.g., *E. hiemale*, the green tissue consists of isolated masses of chlorophyllous cells in the outer part of the cortex below the furrows lying between superficial ridges. The latter are composed of thick-walled fibers (sclerenchyma) which give rigidity to the shoot, and the sclerenchyma also extends between the masses of green cells. The rest of the cortex is composed of thin-walled parenchyma.

The branches have essentially the same structure as the main axis but are much more slender, and the central cavity may be absent. This is also the case in the slender shoot of *E. scirpoides*. The leaf sheaths in the latter have only three teeth, and in the branches of the larger species there is a reduction in the number of teeth. In the more slender branches

the cortex is composed of spongy green parenchyma and the vallecular canals are not developed.

Each leaf has a very simple collateral bundle which is continued as a leaf trace into the internode, where it joins the internodal bundle at a point below the node. The bundle of the leaf has no carinal canal and the tracheary tissue is poorly developed.

The stomata in Equisetum are very characteristic. They are usually confined to the furrows of the internodes; but there are some exceptions. In Eucquisetum the stomata are flush with the surface of the epidermis, but in Hippochaete the stoma is sunk below the surface of the epidermis and opens into a chamber covered by a silicious membrane. In addition to the typical guard cells there are two lateral accessory cells which overarch and almost completely conceal the true guard cells, so that the orifice of the stoma is sunk in a narrow cleft. The inner walls of the guard cells have conspicuous transverse silicious bars. Milde divides Equisetum into Equiseta phanopora (= Eucquisetum) and E. cryptopora (= Hippochaete).

THE ROOT

Each bud which is to develop into a branch normally produces the rudiment of a root at its base, but the roots usually remain dormant and only those from buds at the nodes of the rhizome are functional. Though the roots are probably always of endogenous origin, this has not been certainly proved. The buds formed on the rhizome may develop into aerial shoots, in which case roots will develop from the basal nodes; or the buds may remain undeveloped except for a root formed from its basal node.

The vascular cylinder of the root is either triarch or tetrarch; i.e., in cross section there are either three or four xylem masses alternating with as many phloems. There is a single large vessel in the center of the stele, which is recognizable at a very early stage in its development. There is a conspicuous endodermis, which becomes divided by periclinal walls into two layers. Numerous root hairs are present.

Secondary roots may be formed, each arising endogenously from a cell of the endodermis which is in contact with the xylems of the root stele. The young root pushes through the overlying tissues and emerges at the surface of the root.

THE STEM

The apex of the young shoot shows a large tetrahedral cell the divisions of which are extremely regular. From the lateral faces segments are cut off in regular succession, and each segment is divided by a horizontal wall into two similar superposed semi-segments. Each cycle of three segments

is thus divided into two tiers, the upper forming the node, the lower the internode. Owing to a slight displacement of the young segments the leaves of succeeding nodes alternate.

The tissues of the young shoot show an early differentiation into a central cylinder and the cortex. With the rapid growth the central tissue, the pith, becomes torn apart and, except at the nodes, forms the large central cavity which is found in the internodes. The pith remains intact at the nodes, where it forms a diaphragm separating the internodes.

In the cortex is a zone of actively dividing cells, the "procambium," in which are soon evident the beginnings of the ring of vascular bundles cor-

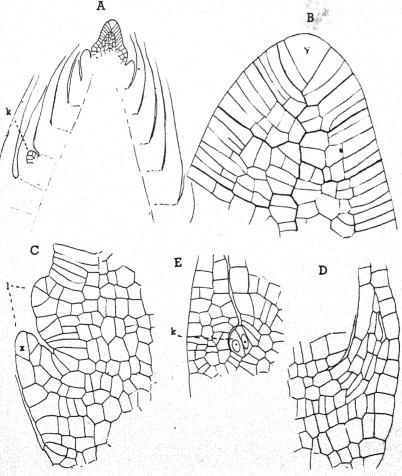


Fig. 140.—A, B, stem apex of Equisitum maximum; x, apical cell; k, lateral bud; C, D, leaf development; E, k, young lateral bud.

responding to the number of leaves formed at the node. Outside the young vascular bundles and alternating with them in the cortex are formed the "vallecular canals." The first tracheary tissue, the protoxylem, appears on the inner side of the young bundle. These primary tracheids are later destroyed by the formation of the carinal canal to whose walls adhere the rings derived from the ruptured protoxylem tracheids.

The apex of the young shoot is enclosed in the closely imbricated leaf

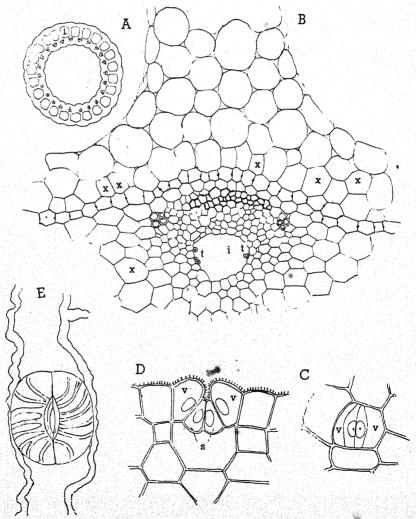


Fig. 141.—A, cross section of internode of E. maximum; B, vascular bundle of internode; i, lacunae; t, primary tracheids; x, tannin cells; C, young stoma; v, accessory cells; D, vertical section of an older stoma of E. limosum; s, guard cells; E, inner surface of an older stoma.

sheaths of the younger nodes. The very young sheath is a circular ridge formed from the outer tissue of the node. The growth of the sheath is due in great part to the activity of a row of marginal cells in which a regular segmentation occurs. At definite intervals the growth is more active and marks the beginning of the individual leaves, or teeth. In E. scirpoides, the smallest species, there are always three teeth, but in the larger species the number is much greater. In E. maximum there are twenty to forty. Sometimes the increase in number is due to a dichotomy of some of the primary teeth.

A longitudinal section of a very young leaf shows an axial strand of elongated cells, the beginning of the vascular bundle. The bundle of the young leaf bends downward at its base and joins the procambium cylinder of the internode.

BRANCHES

A longitudinal section of the stem apex of the sterile shoot of *E. arvensis* or *E. maximum* shows very clearly the origin of the lateral branches. The bud originates from an epidermal cell of the axis close to the base of the young leaf. In this cell three intersecting walls cut out the tetrahedral apical cell of the future branch, whose subsequent development is like that of the main axis. While still very small the young bud is enclosed in a cavity at the base of the leaf sheath which becomes coalescent with the surface of the stem. The young branch breaks through the base of the leaf sheath so that it seems to have been formed endogenously, like a root, and to have originated below the leaf sheath and not in its axil.

THE ROOT

Like the stem, the root has a tetrahedral apical cell with very regular divisions. Segments are cut off from all faces, the lateral ones contributing to the central stele, the cortex and epidermis. From the terminal segment the root cap is formed. Each lateral segment first divides by a radial wall into two nearly equal cells; and in each of these, by a periclinal wall, an inner cell is cut off. The six central cells thus formed belong to the "plerome," from which the axial stele of the root is developed. By a later periclinal wall in the outer cells, the epidermis is separated from the cortex. The cap segment divides first into equal quadrants, which later undergo both vertical and periclinal divisions such that the limits of the early segments can no longer be recognized.

In the axis of the stele is a row of cells which can be recognized at a very early stage. These later coalesce into a large central vessel. A definite endodermis separates the stele from the outer cortical tissue. The endodermis later is divided into two layers. A cross section of the very young stele shows the large central vessel surrounded by a single row of usually six

or eight cells which later become differentiated into alternate masses of xylem and phloem. The root is therefore either triarch or tetrarch. The walls of the tracheary elements of the older root have spiral thickenings; the phloem is composed of sieve tubes and thin-walled parenchyma. It is generally assumed that no pericycle is developed, but perhaps the "inner endodermis" might be interpreted as a pericycle. The secondary roots develop from cells of the inner endodermis which are in contact with the xylem.

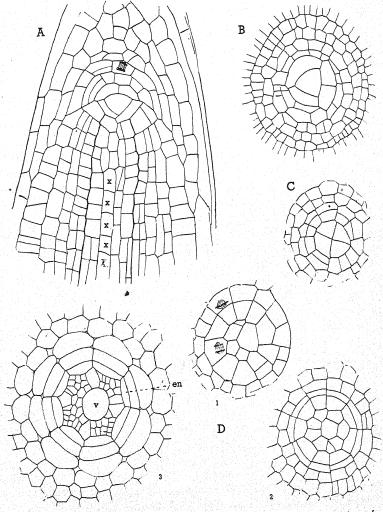


Fig. 142.—A, root apex of $Equisetum\ maximum$, the central row of cells, x, unite to form a large axial vessel; B, cross section of the root apex; C, first division in the root cap; D, three sections of the young vascular bundle; v, the large central vessel; en, endodermis.

THE SPORANGIUM

The sporangium of Equisetum differs greatly from that of the Lycopodineae. The sporangia are borne on very characteristic sporangiophores, which form a compact cone at the apex of the fertile shoots. They are in whorls about the nodes of the strobilus, in which the internodes are almost completely suppressed, so that the sporangiophores are crowded together. Each sporangiophore is composed of a short stalk which supports a flattened, peltate disc, from the margin of which depend the sac-shaped sporangia. Owing to the crowding of the sporangiophores, they have a nearly regular hexagonal outline as seen on the surface of the cone.

med.

The young sporangiophore is a nearly hemispherical body which becomes constricted at the base to form a short stalk with the sporangiumbearing disc at its summit. The sporangium arises near the margin of the disc. A large superficial cell can sometimes be seen which divides into an outer and inner cell; the latter is the primary sporogenous cell, or archesporium. The outer cell divides again by a periclinal wall. Whether all of the sporogenous tissue comes from the primary archesporial cell is not entirely clear. Bower, who has made a critical study of this point, concludes that the inner of these two cover cells also contributes to the sporogenous complex. In the meantime the young sporangium grows rapidly and projects downward from the margin of the disc. The large mass of archesporial tissue is not very clearly defined and is surrounded by three or four layers of sterile cells which form the sporangium wall. The cells in contact with the sporogenous tissue function as a tapetum and are broken down and contribute to the growth of the developing spores. When the sporangium is ripe, only the outer layer of the wall remains intact. The cells develop spiral and annular thickenings on their walls, which recall the structure of the endothecium of the anthers of the angiosperms.

The spore mother cells are for a time united in groups, but become entirely free before the first division of the nucleus. The mother cells are surrounded by the protoplasmic contents of the broken-down tapetum, whose nuclei remain intact and are doubtless active in the nourishment of the developing spores. The reduction division (meiosis) is followed by the division of the daughter nuclei—the four resulting nuclei being arranged tetrahedrally in the mother cell. Simultaneous formation of cell walls between the nuclei results in the completion of the spore tetrad. The spores at once become globular but show no indication of the tetrahedral form exhibited by most spores of this type.

The young spore has a thin cellulose membrane (endospore) outside of which are developed two layers—a middle lamella (exospore) and an outer "epispore"—the latter directly formed from the activity of the tapetal nuclei. The epispore splits spirally into two narrow bands which re-

main attached to the exospore at their middle points. The ends of these bands are spoon-shaped. These are the "elaters" peculiar to the spores of Equisetum. The ripe spores contain abundant chlorophyll. The very marked hygroscopic movements of the elaters are doubtless a factor in the dehiscence of the sporangium and the scattering of the spores. As the sporangia ripens, the cells lose their moisture and the sporangium wall shrinks, so that a longitudinal cleft is formed on its ventral side through which the spores are discharged.

The spores germinate quickly and the first cell division may be completed in ten or twelve hours. The spores soon lose their viability, and after two or three weeks will not germinate. The two cells are of unequal size, the smaller one elongating and forming a rhizoid. The large cell

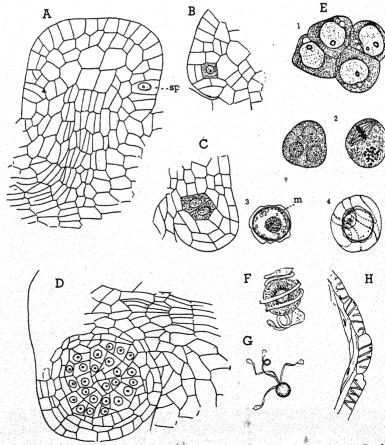


Fig. 143.—A, young sporangiophore of E. maximum; B, C, young sporangia; D, older sporangium; E, spore division; F, G, spores and elaters; H, wall of sporangium.

which contains most of the chlorophyll increases in size and undergoes repeated division, but these show a good deal of variation. Sometimes a definite apical cell can be demonstrated but usually this is not the case. The gametophyte may be a branching thallus composed of a single layer of cells, but more often it develops a more compact cylindrical body several cells in thickness attached to the substratum by several rhizoids at the base. From the anterior region are developed leaf-like lobes and a definite growing point. There is a good deal of difference in the gametophytes of Euequisetum and Hippochaeta. In E. arvense and E. maximum, representing Euequisetum, the young gametophyte is a dorsi-ventral struc-

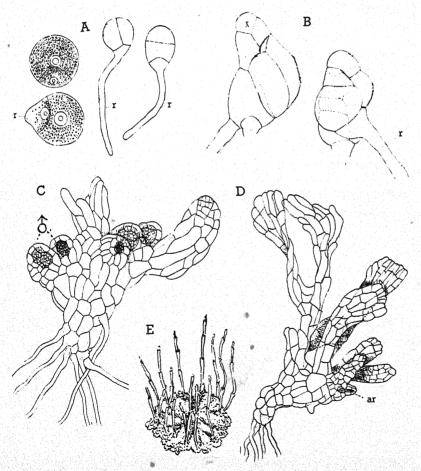


Fig. 144.—A, germinating spores of E. maximum; r, rhizoid; B, young gametophytes of the same; C, male gametophyte; D, female; E, gametophyte of E. debile, hearing several young sporophytes.

ture which might be compared to such a liverwort as Fossombronia or to Dendroceros of the Anthocerotes, which have a central midrib and lateral irregular leaf-like lobes. In the older gametophyte of E. arvense and E. maximum the apex develops a marginal meristem with several growing points, probably the result of repeated dichotomy. In E. laevigatum and E. debile, representing the section Hippochaete, the gametophyte is very much larger than in E. maximum, sometimes forming a cushion 3 centimeters in diameter. Miss Walker states that in E. laevigatum the marginal meristem is more active at some points than at others, forming a number of marginal lobes. The gametophyte of this type is probably a more primitive one than that of Eucquisetum, e.g., E. maximum. It is a compact round cushion composed of many closely set upright lobes. Around the margin is a zone of meristem tissue, probably the result of repeated dichotomy of the primary apex. This cushion might be compared to the circular cushions formed by many Hepaticae, e.g., Riccia, which grow under similar conditions. The comparison with the erect, radially symmetrical gametophyte of Lycopodium cernuum suggested by Kashyap requires for its acceptance a more detailed study of the origin of the meristem than has yet been made.

GAMETANGIA

In E. maximum and E. arvense the gametophytes are normally dioecious, archegonia and antheridia rarely being found on the same prothallium. In E. debile and E. laevigatum the gametophyte is monoecious.

In E. maximum and E. arvense the male gametophyte is smaller than the female. In E. maximum the first antheridium appears in about a month after the spores are sown. The antheridia may develop singly at the apex of branches of the prothallium, or they may develop from a definite marginal meristem at the apex of the gametophyte where they are formed in regular acropetal succession. The mother cell of the antheridium divides into an outer cover cell and an inner cell from which the mass of spermatocytes is formed. The cover cell, by repeated divisions, forms a single layer of cells. Sometimes a triangular operculum cell is present, as in Lycopodium phlegmaria.

Owing to their large size, the spermatozoids of *Equisetum* are especially favorable for a study of spermatogenesis. Before the final division in the spermatogenic cells there may sometimes be seen two blepharoplasts near the nucleus. These later occupy the poles of the nuclear spindle and after the division is complete one goes with the nucleus of each spermatocyte.

The globular nucleus of the spermatocyte becomes elongated and forms a flattened band tapering at the ends and spirally twisted. Surrounding the nucleus is an envelope of cytoplasm. The blepharoplast becomes greatly elongated and finally forms a spirally coiled, deeply staining filament ex-

Car feet X

tending beyond the nucleus. According to Sharp, the blepharoplast is made up of separate granules which finally coalesce into a continuous filament. From the blepharoplast the numerous cilia develop. The spermatozoid of Equisetum thus differs essentially from the biciliate spermatozoids of Lycopodium but may be compared with that of Psilotum. It still more nearly resembles the spermatozoid of the lower ferns. While the greater part of the spermatozoid is derived from the nucleus, there is an envelope of cytoplasm and there may be attached to the large posterior coil of the free spermatozoid a vesicle containing the remains of the cell cytoplasm.

The young female gametophyte in *E. maximum* is a cylindrical body bearing lateral leaf-like lobes. After the archegonia begin to develop and a

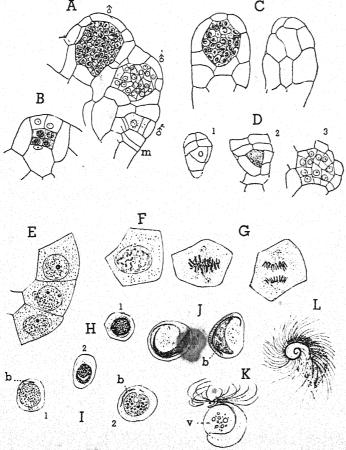


Fig. 145.—A-D, development of the antheridium of E. maximum; E, spermatogenic cells; F-I, development of the spermatozoids; K, free spermatozoid; b, blepharoplast (I, L, after Belajeff).

definite apical meristem is established, the formation of these lobes is very much like that in some of the liverworts. The apical growth of the gametophyte resembles that in many ferns.

The archegonium is formed at the base of a young lobe, on its ventral side; but by the growth of the tissue between it and the apical meristem it is pushed upward and apparently belongs to the dorsal surface of the gametophyte. The first division in the mother cell sometimes separates a basal cell, but usually the first division is like that in the antheridium—dividing the mother cell into an outer cap cell and an inner one. From the latter are formed the egg and canal cells. The cap cell divides by quadrant walls, each of the four quadrants by transverse walls forming a row of three cells which contribute to the neck of the archegonium. The inner cell divides first into a central cell and the primary neck canal cell. The latter divides into two, usually by a transverse wall, but sometimes vertically. In the former case, the upper canal cell pushes between the

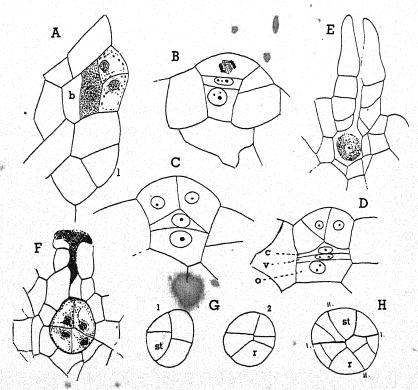


Fig. 146.—A-E, development of the archegonium in E. maximum; F, embryo within the archegonium venter; G, two transverse sections of a young embryo; H, longitudinal section of a somewhat older embryo; st, stem apex; r, root.

elongating neck cells. The terminal cells of the neck become much elongated and when the archegonium opens spread apart and are bent back. From the central cell are developed the egg and ventral canal cells.

THE EMBRYO

Usually more than one archegonium is fertilized and several normal sporophytes may be developed. This is especially marked in *E. debile*, where Kashyap reports as many as fifteen borne by a single gametophyte. The number of embryos which fail to reach full development is much greater.

There is a good deal of variation in the early development of the embryo. In *E. arvense* and *E. maximum* the basal wall is transverse and this may be the case in *E. debile*, but in the latter there is a good deal of variation and the basal wall may be vertical. The next walls divide the embryo into quadrants, which may be equal in size or unequal. In the latter case, e.g., *E. maximum*, the larger epibasal quadrant becomes at once the apical cell of the shoot.

According to Sadebeck, the apical cell of the primary shoot in *E. arvense* is formed from the primary epibasal cell by three intersecting walls, resulting in the tetrahedral apical cell and three peripheral ones which correspond to the three coalescent leaves of the primary foliar leaf sheath. In *E. maximum* the condition is essentially the same as in *E. arvense*.

With the establishment of the growing point of the shoot the further growth of the young sporophyte is essentially like that of the mature plant. The three teeth of the primary leaf sheath grow rapidly and enclose the stem apex. With the formation of new leaf sheaths and the elongation of the internodes the young shoot soon shows the characteristic jointed habit, each node surrounded by a three-toothed sheath.

The hypobasal region in *E. arvense*, according to Sadebeck, shows definite root and foot quadrants, and the large initial cell of the root has a cap cell cut from its outer face. The growth of the primary root is slow and it does not emerge until the shoot has reached considerable size. The foot is not conspicuous in the early stages of development and its limits are not well defined.

In *E. debile*, belonging to the section *Hippochaete*, the early divisions of the embryo are less regular than in *E. arvense*. While there may be a division into equal quadrants, in most cases studied by the writer, the epibasal portion was smaller than the hypobasal and the stem apex is not differentiated so early as in *E. arvense*. In the hypobasal region no definite succession in the divisions could be demonstrated and there was some indication of a root primordium. In most cases the whole hypobasal region appeared to represent a foot, and the embryo at this stage is somewhat

flattened in form and shows a marked resemblance to the embryo of some of the Marattiales, a primitive group of ferns. Buchtien figures a somewhat similar condition in *E. variegatum*, also a species of *Hippochaete*.

The stem apex is first recognizable as a conical prominence with the characteristic tetrahedral apical cell. The further development of the shoot is much like that of the other species that have been investigated.

The origin of the primary root in *E. debile* is not quite clear. The limits between the epibasal and hypobasal regions are indistinguishable in the older embryo. Jeffrey claims that in *E. hiemale* the root arises from the epibasal region and possibly this may be the case in *E. debile*.

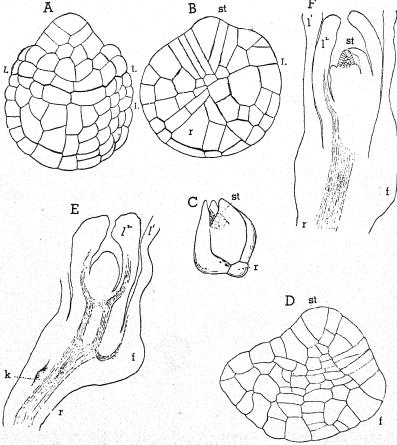


Fig. 147.—A, surface view of an advanced embryo of E. arvense; B, optical section of a similar stage in E. palustre; C, older embryo of E. arvense; D, nearly median section of embryo of E. debile; st, stem apex; f, foot; E, F, section of older stages of E. debile; in E, an endogenous bud, k, is formed near the base of the primary root (A-C, after Sadebeck).

The young shoot elongates rapidly and emerges on the upper side of the gametophyte, while the primary root penetrates the gametophyte and fastens the young plant to the substratum. The further development of the primary shoot is practically the same as that of the adult sporophyte. As a rule the sheaths of the primary shoot have three leaves, but sometimes there may be two or four.

The large foot merges with the base of the first foliar sheath, and the root is very evident; but it is impossible to tell how much of the hypobasal tissue belongs to the foot and how much to the root. A section of an internode of the shoot shows three vascular bundles corresponding to the three leaves of the foliar sheath. At the basal node the leaf traces unite into a complete ring. The root shows a triarch structure corresponding to the three traces of the basal foliar sheath.

In Equisetum the primary shoot has a limited growth and the further development of the sporophyte is from a bud formed at the base of the primary shoot. In E. debile this bud is formed not from the shoot itself but from the primary root. Whether or not this is true for other species remains to be determined. The origin of this bud is exactly like that of a secondary root; i.e., it is endogenous, originating near the stele of the root and later breaking through the cortical tissues of the root. This secondary

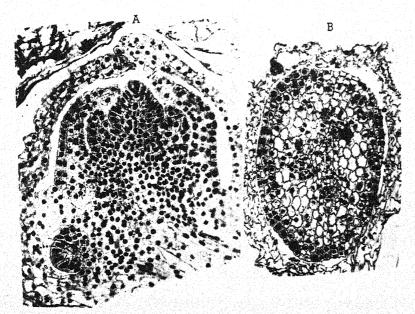


Fig. 148.—A, endogenous bud, k, forming at the base of the primary root in E. debile; B, cross section of the young sporophyte of the same, showing the three primary vascular bundles (photographs by Mr. L. H. Daugherty).

shoot, while still quite young, develops a similar endogenous bud which forms the third shoot of the plant. Whether or not the succeeding shoots arise in similar fashion has not been investigated. Finally, a shoot, instead of assuming the upright position of the earlier ones, becomes prostrate, penetrates the ground, and becomes the permanent rhizome from which the aerial shoots of the adult plant are produced. The possibility that these later shoots may also arise endogenously might be considered.

The great similarity in the origin of the roots and buds in the young sporophyte emphasizes the slight difference in the essential nature of the root and shoot. From a study of the origin of the vascular bundles in the young sporophyte of *E. debile* and the mature shoots of other species, the conclusion may be reached that in the shoot of *Equisetum* there is no single stele but the internodal strands are made up of united leaf traces.

RELATIONSHIP OF THE EQUISETACEAE

Of the two sections of the genus Equisetum, Euequisetum and Hippochaete, the latter is probably the more primitive. The development of the special fertile shoots in Euequisetum may be considered as a secondary condition when compared with the condition in Hippochaete; but some species of Euequisetum, like E. pratense, are intermediate in character. Like E. arvense, the fertile shoots arise in the spring but, instead of withering after the spores are shed, green branches are produced much as in the sterile shoots of E. arvense and E. maximum. The cones in Hippochaete have a sharp point.

The embryo in *Hippochaete*, so far as data are available, differs from that of *E. arvense* in showing much less regularity in the early divisions and in a later differentiation of the organs, especially the root. These characters also suggest that *Hippochaete* is a more primitive type than *Euequisetum*. This is also indicated by the very large gametophyte in *E. debile* and *E. laevigatum*.

There has been a good deal of speculation concerning the relationships of Equisetum with the other living pteridophytes. Some investigators, e.g., Jeffrey and Scott, have concluded that the Equisetineae are sufficiently similar in structure to the Lycopodineae to warrant the union of the two classes into a common class, "Lycopsida," opposed to the Pteropsida, which includes the ferns and their allies. This view assumes that the vascular systems of Lycopodium and Equisetum are homologous—i.e., the whole vascular system of the stem of Equisetum is a single "stele." Other assumed common structural details are the leaves and the strobili. The gameto-

phytes are also considered to have a similar structure. Van Tieghem, however, describes the vascular system as "astelic," like that of the primitive fern, *Ophioglossum*. Examination of the origin and development of the vascular bundles, seen in sections of the growing point of the shoot, both in the primary shoot of the young sporophyte and in the mature plant, clearly indicates that the internodal bundles are composed of united leaf traces and, moreover, these bundles are in the cortical region of the shoot. The central "stele," if it may be so designated, contributes only to the pith. The condition in Equisetum is rather comparable with that in many ferns, e.g., the Mariattiaceae, where the complicated vascular system of the axis is composed mainly of the fusion of numerous leaf traces. The much simpler condition in Equisetum may perhaps be associated with the much-reduced leaf structures.

The gametophyte and embryo of *Equisetum* have much more in common with the lower ferns than with the Lycopodineae. This is true also of the gametangia, especially the large multiciliate spermatozoids which closely resemble those of the lower ferns and differ greatly from the small biciliate sperms of *Lycopodium*.

In short, while any relationship between Equisetum and any living ferns must be extremely remote, it is not inconceivable that the two phyla, Equisetineae and Filicineae, may have diverged from some Devonian stock close to the Psilophyta. The Equisetineae are clearly recognizable as such as far back as the Middle Devonian and have maintained their essential characters with little change to the present time.

FOSSIL EQUISETINEAE

Fossils known as Equisetites and closely resembling Equisetum occur in the Triassic. Much more ancient and presumably more primitive types are found in the Upper Devonian and the Lower Carboniferous. Still more ancient forms showing evidences of relationship with the Equisetineae have been described from the middle of the Devonian. Especially important in this connection is the work of Kraüsel and Weyland. These Devonian fossils are apparently related also to the Psilophyta and have characters suggestive of both the ferns and the horse-tails. Two of these, Hyenia and Calamophyton, have been placed in a special class—Protoarticulatae.

Hyenia has a fan-shaped body suggesting the frond of a fern, but the branches were beset with slender dichotomously branched appendages, some of which were sporangiophores bearing pendent sporangia, recalling the sporangiophores of Equisetum. Calamophyton resembles Hyenia in general form but had its main branches distinctly jointed, and at the nodes of some of the lateral branches were whorls of small forked leaves, comparable to those of Asterocalamites. Other branches bore sporangia much like those of Hyenia.

It is quite conceivable that from forms resembling Hyenia and Cala-

mophyton, with their fern-like fronds, there was developed in one direction the typically megaphyllous ferns, and in another the primitive Equisetineae like Asterocalamites, with relatively large, dichotomously divided leaves. With the progressive reduction of the leaves and the predominance of the stout axis it may be surmised that the condition in Equisetum was developed.

Certainly belonging to the Equisetineae is the genus Asterocalamites (= Archaeocalamites), a characteristic genus of the Late Devonian and the

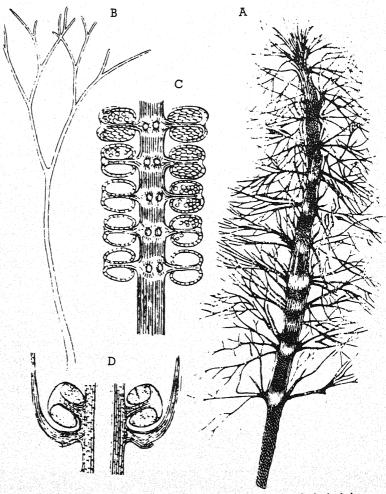


Fig. 149.—Fossil Equisetineae. A, Archaeocalamites radiatus; B, single leaf of the same; C, sporangiophores (diagrammatic); D, sporangiophores of Palaeostachya (A-C, from Scott, after Stur; D, from Scott, after Renault).

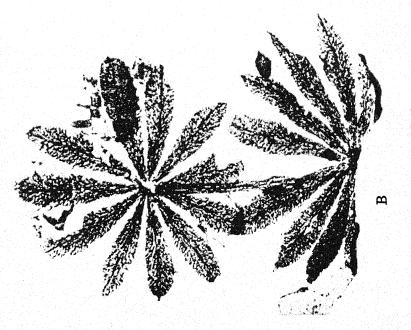
Early Carboniferous. The stout axis was developed from a rhizome much like Equisetum, and circles of branches surrounded the nodes. The leaves were relatively large, were not joined in a sheath, and were divided dichotomously into several narrow segments. They were evidently functional. Unlike Equisetum, the whorls of leaves here did not alternate in succeeding nodes. The sporangia were in groups of four on a shield-shaped sporangiophore, much as in Equisetum, and the sporangiophores formed a cone at the end of a shoot. It is likely that Equisetum is descended from some form not unlike Asterocalamites, from which it differs mainly in the character of leaves.

From the Asterocalamites type it is likely that the Calamariaceae, the largest and most specialized members of the class, were also derived. These were an important element in the later Palaeozoic floras, especially the Carboniferous.

Notable among these were the species of Calamites which, with a stem structure much like Equisetum, reached tree-like dimensions. As in Equisetum there was here a subterranean rhizome from which the aerial shoots developed. Whorls of branches surrounded the nodes of the main axis, and these bore secondary branches. The smaller branches had whorls of free, narrow leaves and the detached branchlets, with their circles of leaves, were first described as an independent genus, Annularia.

The arrangement of the vascular bundles of the stem in Calamites is exactly like that in Equisetum and the structure of the bundles in the young shoots very much the same; but later a peripheral cambium was developed and secondary xylem and phloem were formed. The older stem shows a woody cylinder with medullary rays, much like the woody cylinder in coniferous and dicotyledenous trees. No evidence of seasonal growth rings has been found, indicating that the growth was uninterrupted. There was an active zone of meristem or "periderm" in the cortex which thus kept pace with the increase of the wood. The cones of Calamites are known as Calamostachys. There are whorls of sporangiophores much like those of Equisetum, but alternating with them are circles of bracts. Where spores have been found they are all alike; but heterospory has been shown in a few cases, though less developed than in the Lycopodineae. At present no evidence of seed formation has been discovered in the Equisetineae.

Several specialized lines have diverged from the main phylum of which Calamites seems to represent the culmination. Perhaps the most important of these lines is the order Sphenophyllales, which is first met with in the Devonian and persists into the Early Mesozoic (Triassic). The Sphenophyllales were probably herbaceous plants with slender jointed stems. Leaves of two kinds have been described, those developed from the lower nodes of the stem being finely divided and those from the upper nodes



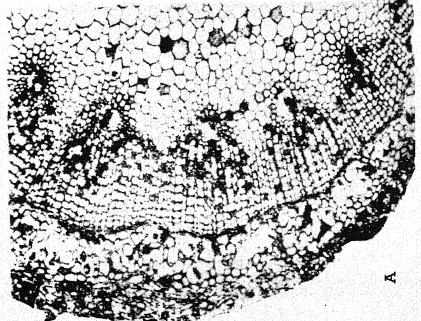


Fig. 150.-4, section of young stem of Calamites sp.; B, Annularia sp. (A, after Scott; B, after Walton).

entire but with dichotomously branched veins. It has been suggested that they may have been partially submersed aquatics like Cabomba or Myriophyllum, where the floating or emergent leaves are entire while the submersed leaves are divided into narrow segments. Seward thinks it more likely that they had a climbing or rather a scrambling habit, like Galium or some brambles.

The stem of Sphenophyllum shows a solid triangular stele with three protoxylems, thus differing much from the typical Equisetineae. In the older stems there is secondary growth due to a cambium.

The strobilus of Sphenophyllum is like that of Calamites—composed of alternate whorls of sporangiophores and bracts, the latter being joined at the base. There is a good deal of difference in the sporangiophores in

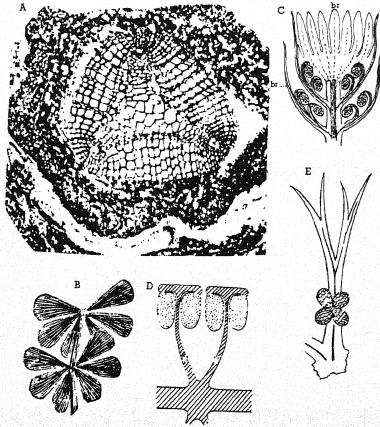


Fig. 151.—A, section of stem of Sphenophyllum insigne; B, S. verticillata; C, diagram of strobilus of S. insigne; br, bracts; D, sporangiophore of fertile S. majus (A-C, after Scott; D, E, Scott, after Kidston).

different species that have been described. In S. fertilis, the long-stalked sporangiophore is expanded at the summit, somewhat like Equisetum. There are two sporangia. Sometimes only one sporangium is borne by the sporangiophore. The sporangiophore is adherent to the base of the subtending bract. Most species that have been examined are homosporous, but S. verticillata is heterosporous.

Other fossil types belonging to the class are *Phyllotheca* and *Schizoneura*, both ranging from the Late Carboniferous to the Jurassic. In the former the leaves are in a whorl partially united at the base; in *Schizoneura* they are in two groups at each node, the leaves almost completely

united.

CONCLUSION

The Equisetineae form an extremely ancient and natural assemblage which has persisted up to the present time. Equisetum, or its equivalent fossil form, Equisetites, can be traced back to the Triassic and retains its primitive characters except for the reduced leaves. All of the older forms show functional leaves having either dichotomous venation or actual forking of the leaf. The Equisetaceae probably branched off from the main stock near its beginning, and the living forms are to be considered as reduced not from the large specialized types of the later Carboniferous but from Late Devonian or Early Carboniferous types like Asterocalamites. The Calamites of the Late Carboniferous and Permian mark the high point in the evolution of the class. Heterospory was achieved in some cases, but there is no evidence of seed formation.

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CHAPTER XIII

FILICINEAE—EUSPORANGIATAE: OPHIOGLOSSALES

The Psilotineae, Equisetineae, and Lycopodineae, as they now exist, are evidently remnants of formerly much more extensive groups whose earliest members are found in the Devonian rocks and which reached their highest development in the Carboniferous. The ferns (Filicineae) offer a marked contrast to these and comprise a very large majority of the living pteridophytes. They show a range of size and complexity comparable with the most specialized of their Palaeozoic relatives. The relationships of the living forms with the earlier Palaeozoic types are not so clear as in the other classes.

The ferns are especially distinguished from the other pteridophytes by the character of the leaves, which may reach a size and complexity hardly surpassed by any other group of plants. They reach their maximum development in the tropical rain-forests and in some of the wet low-lands of the South Temperate Zone, as in New Zealand. A few genera are true aquatics—e.g., Ceratopteris, Azolla, and Salvinia—and one species, Acrostichum aureum, grows in salt-water swamps. A good many species are adapted to dry conditions and may become completely dried up for several months, e.g., Californian species of Adiantum, Polypodium, Gymnogramme. Many epiphytic species also are decidedly drought-resistant.

Some of the filmy ferns (Hymenophyllaceae), e.g., *Trichomanes* spp., have slender rhizomes, scarcely thicker than a coarse thread, with fronds less than a centimeter in length; and the Cyatheaceae include tree ferns with stout trunks fifty feet or more in height and gigantic leaves five or

six meters long, rivaling in size the largest fossil species.

From the upper Devonian through the Palaeozoic, fern-like fossils are numerous; but it is not certain how far these are related to the living forms. Whether or not the fern type can be connected with the Devonian Psilophyta is problematical. Of the Devonian Psilophyta, Hyenia and Cladoxylon suggest a possible condition which might connect with the Filicineae. By repeated dichotomy in a single plane the telome of Rhynia might form a plant body without a clear differentiation into stem and leaf. A flattening of the branches of the telome would result in a fan-shaped frond, suggesting the leaves of many living ferns, e.g., Ophioglossum palmatum, Schizaea dichotoma, Matonia pectinata, etc. Of the Devonian fossils, Cladoxylon may possibly represent such an intermediate

type between the Psilophyta and Filicineae. Hirmer places *Cladoxylon* in a special order, Cladoxylales, between the Equisetineae and the Filicineae. Zimmermann unites the Cladoxylales with two other orders, Coenopteridales and Archaeopteridales, in a separate class, Primofilices.

Cladoxylon scoparium was discovered by Kraüsel and Weyland, who figure a restoration based upon their investigations. It was described as probably a low shrubby plant sparingly branched, the branching being

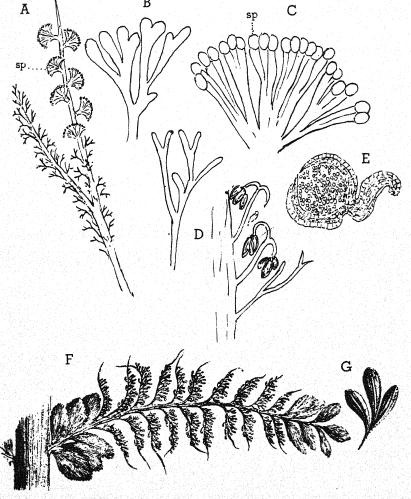


Fig. 152.—A-C, Cladoxylon scoparium; sp, sporangiophores; B, sterile appendages (phylloids); C, sporangiophores; D, sporangiophores of Hyenia elegans; E, sporangium of Stauropteris Oldhamia; F, Archaeopteris hibernica; G, sporangia of Archaeopteris (A-C, after Kräusel and Weyland; D-G, after Scott).

predominantly dichotomous. Some of the ultimate branches bear fertile appendages (sporangiophores). Both sterile and fertile appendages are several times forked. The fertile appendages are fan-shaped with dichotomous venation, closely resembling the leaves of certain ferns. At the apex of each narrow lobe is borne a single sporangium. The anatomy of the shoot, however, is more like that of *Lycopodium*. There is a central stele with several bands of xylem, and surrounding the stele is a thick cortex.

Besides Cladoxylon, whose relationships are problematical, there are other Devonian and Carboniferous fossils which evidently belong to the Filicineae but whose relationships with the existing ferns are by no means clear. Of these fossils the Coenopteridales are the most important. The order includes three families: Botryopteridaceae, Zygopteridaceae, and Anachoropteridaceae. These are to some extent intermediate between the Devonian Psilophyta and the true ferns. They were plants of moderate size and the leaves were not always clearly differentiated from the shoot—a condition suggestive of the Psilophyta.

ORDER ARCHAEOPTERIDALES

From the Upper Devonian and Lower Carboniferous a number of forms have been described which, although they cannot readily be assigned to any of the existing families, are probably true ferns. One of the best known is the genus Archaeopteris, as yet known only from the Upper Devonian. A. hibernica has bipinnate fronds with wedge-shaped pinnules having dichotomous (sphenopterid) venation like that in some living ferns, e.g., Botrychium Lunaria, Anemia, and Marsilea. Oval sporangia with short, thick stalks were borne on the margins and surface of the fertile pinnae in which the lamina is suppressed, recalling the condition in Osmunda. There was no annulus and dehiscence was by a longitudinal cleft as in Osmunda, or the Schizaeaceae.

Our knowledge of the Coenopteridales is still so fragmentary that only a tentative decision can be made as to their relationships among themselves and with the true ferns. It seems fair to conclude that they are in some degree synthetic types with evident relationships with the Devonian Psilophyta, as indicated by their general structure and imperfectly differentiated plant body, as well as their anatomy and the origin of their sporangia.

Whether the Botryopterideae are the most primitive forms, as Bower believes, or the Zygopterideae, which on the whole seem nearer to the Psilophyta, should be so regarded is not quite clear. It is also doubtful whether any of the forms yet discovered are closely related to the ancestors of the modern ferns.

Bower believes there is no reason to doubt that the Coenopteridales should be placed in the Filicineae, though they are generalized rather than specialized types. His conclusion is based upon the external characters, viz., pronounced megaphyllous habit, the anatomical details of the stem, leaf, and root, and the structure and position of the sporangia. There is some disagreement as to the relationships of Archaeopteris, which has been considered by Seward, Kidston, and some others to belong to the pteridosperms and not to the true ferns. Zimmermann includes in the Pteropsida (= Filicineae) all of the modern seed plants as well as the ferns. We shall consider here only the latter as representing the Filicineae.

The living Filicineae may be divided into two main divisions. A relatively small number of the living ferns are characterized by having massive sporangia, sometimes united into synangia which from the first are multicellular. Both the sporangia and the other tissues of the sporophyte are less specialized than in the typical ferns and show a closer approach to the Palaeozoic types. These ferns constitute the "Eusporangiatae" now generally recognized to be the older and more primitive of the living ferns, while the very much more numerous "Leptosporangiatae" are believed to be of later origin. In the latter the sporangium can usually be traced back to a single mother cell.

From a study of the development of the most primitive of the living ferns it seems probable that in their ancestors the sporophyte consisted of a single leaf and a "protocorm" or foot. The root was presumably a later development.

THE OPHIOGLOSSALES

Of living ferns the Ophioglossales most nearly approach this hypothetical ancestral form and are presumably the most primitive of the existing ferns. The order has but a single family, Ophioglossaceae, with three genera, two of which, Ophioglossum and Botrychium, are practically cosmopolitan; the third genus, Helminthostachys, is confined to the eastern tropics. Ophioglossum has a number of species in the temperate regions but is best developed in the tropics. The majority of the species of Botrychium (about 35) are North Temperate, the few tropical species being mostly confined to the higher elevations. A few species occur in the South Temperate zones, e.g., in Argentina, New Zealand, and Australia; and a single species, B. chamaeconium, is found in Africa. Helminthostachys zeylanica, the only species, is found in the lowland forests of the Indo-Malayan regions and tropical Australia.

They are for the most part plants of moderate size; the smallest is only an inch or two in height, and the largest *Ophioglossum*, *O. pendulum*, has leaves sometimes three or four feet in length. Most commonly only a single

leaf develops each season from the apex of the subterranean rhizome. Attached to the leaf, or sometimes almost free from it, is the large sporangiophore, a simple spike with two rows of sporangia in *Ophioglossum* but repeatedly branching in *Botrychium*, where the individual sporangia are borne at the tips of the ultimate branches. Except for two epiphytic species, *Ophioglossum pendulum* and *O. palmatum*, all members of the family are terrestrial.

The rhizome in most cases is short and vertical in position; but in

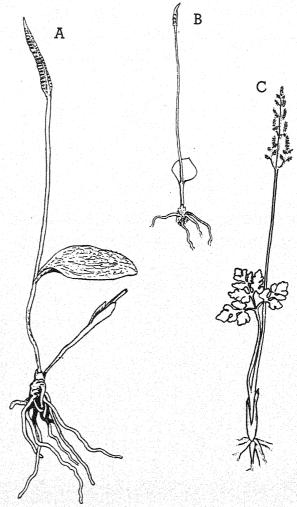


Fig. 153.—A, B, two forms of Ophioglossum moluccanum; C, Botrychium ternatum (C, after Luerssen).

Ophioglossum pendulum and Helminthostachys it is prostrate and dorsiventral in structure. The leaf usually has an elongated petiole or "stipe" and expanded lamina, which in most species of Ophioglossum is entire but in O. pendulum sometimes dichotomously forked; in O. palmatum the fanshaped lamina is deeply cleft into several narrow segments and recalls the digitate frond of some of the kelps, like Laminaria. In some species of Botrychium, e.g., B. Lunaria, the frond is pinnately divided; more commonly it is ternately compound, but the smaller divisions are pinnate. This is also the case in Helminthostachys. The texture of the leaves is in most cases fleshy and the smaller veins are not conspicuous. In Ophioglossum the venation is reticulate, sometimes with free vein endings within the meshes. In Botrychium and Helminthostachys the veins are free or branch dichotomously like those of most of the typical ferns. The roots are relatively stout, and are unbranched in most species of Ophioglossum but more or less branched in the other forms.

There has been a good deal of controversy as to the relation of the sporangiophore and the leaf with which it is associated. Except in Ophioglossum palmatum, where there are several small sporangiophores, the sporangiophore is most commonly borne on the adaxial surface of the frond near the junction of the petiole and lamina. Sometimes, however, it is attached very near the leaf base and apparently quite independent of it.

EUOPHIOGLOSSUM

Except for O. pendulum with two other related species and O. palmatum, representing, respectively, the subgenera Ophioderma and Cheiroglossa, all the species are included in the subgenus Euophioglossum. These are much alike in general appearance and anatomical structure. The sporangiophore has a long peduncle, often much exceeding in length the lamina of the leaf. It is usually attached near the base of the lamina, which varies in outline. The venation is reticulate. In most of the species there is a system of large closed meshes, within which are secondary branching, free veins. In a few cases, e.g., O. lusitanicum, the free veins are absent.

The rhizome bears numerous unbranched roots without root hairs. In most species a single leaf is developed each season; but in some tropical species where growth is uninterrupted, more than one leaf may develop. Where growth is seasonal, as in the Temperate Zone, the development of the leaf is very slow. Thus in O. vulgatum the leaf does not emerge until four years from the time it can first be recognized in the bud. It is hardly likely that in the rapidly growing tropical species the development of the leaf is so slow.

A longitudinal section of the stem apex in O. moluccanum shows the growing point to be completely enclosed in a cavity formed by the conical

stipular sheath at the base of the youngest leaf. The apical cell of the stem seen in cross section is either three- or four-sided, and the base is truncate. The stipular sheath has a narrow pore at the top, opening into the space between it and the sheath of the next older leaf. Three leaves of different ages, each enclosed in the sheath of the next older one, can be seen in a median longitudinal section of the stem apex.

From each leaf a strand of procambium passes into the cortical region of the stem and joins the bundle from the next older leaf. There is thus built up an open, large-meshed, fibro-vascular reticulum. No fibro-vascular bundles are developed directly from the apical meristem of the axis, and the whole fibro-vascular system is formed from the union of leaf traces.

In cross section of the stem the vascular strands appear as a circle of small collateral bundles without any endodermis, the xylem being in direct contact with the parenchyma of the ground tissue or at most with a single layer of pericycle cells. In some of the smaller species the leaf traces are relatively broader and suggest an approach to the condition found in

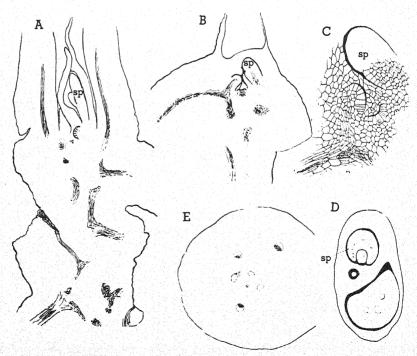


Fig. 154.—A, longitudinal section of mature sporophyte of *Ophioglossum moluccanum*; sp. young sporophyll; B, section of stem apex and young sporophylls; C, the same more highly magnified; D, cross section of young leaf sheath; sp. sporophyll; E, cross section of the adult rhizome.

Botrychium and Helminthostachys. In the outer cortex there may be a limited development of periderm which probably belongs to the old leaf bases.

The leaf.—The leaf structure in Euophioglossum is very simple. Stomata are developed on both surfaces, and the mesophyll is practically uniform throughout and is traversed by the delicate anastomosing veins. In the petiole of the fertile leaf of the smaller species there are three vascular bundles, two adaxial and one abaxial. From the latter the veins of the lamina are derived, while the two adaxial bundles extend into the peduncle of the sporangiophore. At the leaf base the bundles coalesce into the single leaf trace, which passes into the stem and joins the complex of bundles formed by the older leaf traces. In O. moluccanum there are four bundles in the petiole—three adaxial and one abaxial. Of the three adaxial bundles the central one extends into the peduncle of the sporangiophore, the two lateral ones also contributing to the vascular system of the sporangiophore; but from the lateral branches there are also formed secondary branches which supply some of the veins of the lamina. Under these conditions to consider the sporangiophore as an appendage of the lamina seems hardly warranted.

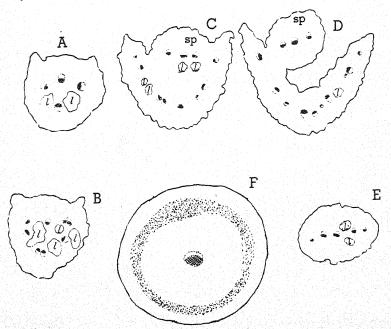


Fig. 155.—A-E, five sections of the sporophyll of O. moluccanum: A, the petiole, B, C, D, intermediate, E, stalk of the sporangiophore; F, section of root showing monarch vascular bundle, and zone of mycorrhizal cells.

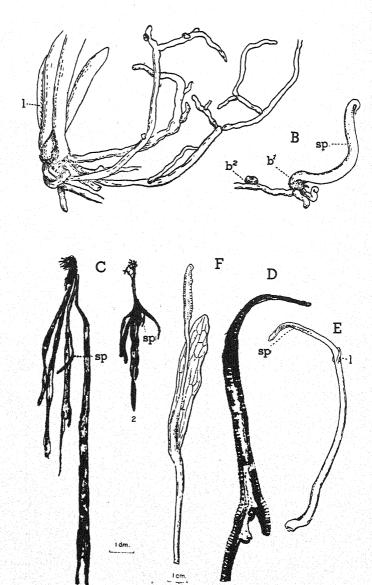


Fig. 156.—A, rhizome of Ophioglossum pendulum, showing leaf bases and much branched roots; B, root fragment bearing two buds, b', with young sporophyll; C, two mature plants, greatly reduced; D, sporangiophore of O. pendulum; E. F, O, intermedium; in E, the lamina of the sporophyll almost completely suppressed.

The root.—The stele of the root in Euophioglossum is in most species monarch. About two-thirds of the bundle is occupied by the solid mass of xylem. The pericycle consists of a single cell layer, but the endodermis is not clearly differentiated. The cortex is composed of simple parenchyma, and there is a broad zone where the cells are occupied by an endophytic fungus which is also found in the gametophyte. The first roots of the young sporophyte of O. pedunculosum have a large tetrahedral apical cell with pretty regular segmentation; but the divisions in the root cap are less regular than in the typical ferns. In roots from the mature plant the segmentation of the apical cell seems to be less regular than in the younger sporophyte.

OPHIODERMA

Ophioglossum pendulum, the best-known representative of the subgenus, is the largest member of the family. It is not uncommon in the eastern tropics and occurs also in Hawaii and northern Australia. It is an epiphyte growing on the trunks of tree ferns and palms and also rooted in the moss

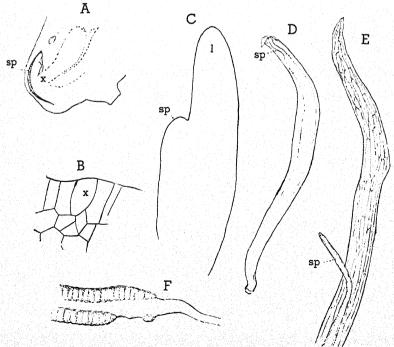


Fig. 157.—A, section of stem apex of Ophioglossum pendulum, with young sporophyll; B, the stem apex; C, sporophyll, more enlarged; D, E, young sporophylls; F, mature sporangio-phore.

of humus between the old leaf bases of large epiphytic ferns, especially Asplenium nidus.

The stout rhizome is dorsi-ventral and the leaves form two series on the dorsal side. The pendant, strap-shaped leaves have a short petiole, which merges gradually into the lamina. The larger leaves may fork once or twice. Sometimes each of the two divisions may bear a sporangiophore. The roots branch freely in contrast to those of *Euophioglossum*.

The sporangiophore has a short peduncle, which is continued into the short, thick petiole of the leaf. Above the insertion of sporangiophore the lamina is of uniform thickness and the sporangiophore appears to be at the apex of the thickened leaf base to which the lamina is adherent. In a second species, O. intermedium, a much smaller terrestrial species evidently related to O. pendulum, the lamina is much reduced in size and sometimes almost entirely suppressed, so that the terminal character of the sporangiophore is even more evident. In O. simplex, according to Bower, the lamina is entirely wanting.

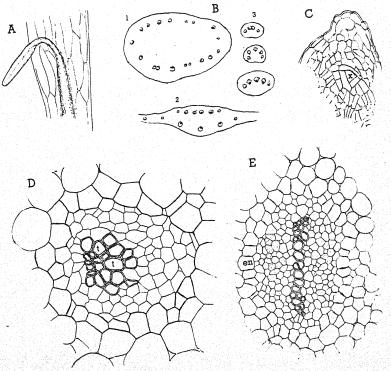


Fig. 158.—A, young sporangiophore and base of leaf lamina of Ophioglossum pendulum; B, cross sections of sporophyll: B, I, petiole, B, 2, intermediate, B, 3, peduncle of sporangiophore; C, root apex; D, vascular bundle of petiole; E, root; en, endodermis.

The leaf.—The apical growth of the stem in O. pendulum differs much from that in Euophioglossum. The young leaf breaks through the enclosing sheath while still in a rudimentary condition. A section through the base of the young leaf shows only a single younger leaf within, instead of the three or four in the bud of Euophioglossum. The numerous vascular bundles of the petiole do not unite into a single leaf trace but pass downward separately through the cortex of the rhizome. In the petiole the bundles anastomose freely, forming elongated meshes like those in the lamina. A section of the rhizome shows a nearly complete ring formed by the fusion of the bundles from the numerous leaf traces. There is thus a greater development of woody tissue in the rhizome than is the case in Euophioglossum.

The vascular bundles of the petiole are much like those in *Euophioglossum*, but there is a somewhat greater development of parenchyma on the inner side of the bundle, suggesting an approach to the concentric bundle found in the petiole of *Botrychium*.

The root.—The roots of Ophioglossum pendulum differ anatomically from those of Euophioglossum. Instead of the stele being monarch, it varies from diarch in the primary root to triarch, tetrarch, or even pentarch in some of the larger roots.

The sporophyll.—The young sporophyll in O. pendulum has a massive basal portion terminating in the young sporangiophore, the lamina of the leaf being rudimentary and evidently a secondary development.

CHEIROGLOSSA.

Ophioglossum palmatum, the only representative of the section Cheiroglossa, is an epiphytic species from tropical America reaching to Florida, and also reported from the Seychelles and Bourbon in the Indian Ocean. The large, palmately divided leaves have the venation of the Euophioglossum type. In some of the smaller fertile fronds there is a single median sporangiophore; but in the larger fronds there are several small sporangiophores forming a series on each side of the petiole, usually below the base of the lamina, but occasionally above the base. According to Bower they are always attached to the adaxial face of the petiole and are not strictly marginal in position.

The roots are more slender than those of *O. pendulum* and much less freely branched. There is some evidence that the branching may be a true dichotomy, such as sometimes occurs in *Euophioglossum*. The roots are usually diarch but the largest are triarch.

The sporangiophore.—In Euophioglossum the sporangiophore can be recognized at a very early stage in the development of the sporophyll. Almost as soon as the latter can be seen there is a division into two practically

equal parts, one of which develops into the sporangiophore, while from the other the sterile leaf segment is formed. The sporangiophore therefore is not to be considered as an appendage of the leaf but as co-ordinate with it. A comparison might be made with the dichotomy of a telome into fertile and sterile branches, such as occurs in some of the Rhyniaceae. That the sporangiophore is more important than the sterile leaf segment is indicated by the diversion of the major part of the fibro-vascular tissue of the petiole into the sporangiophore.

The fertile region of the sporangiophore is a flattened spike with the large sporangia along the margins. The masses of spores are separated from the surface by several layers of cells forming the outer wall of the

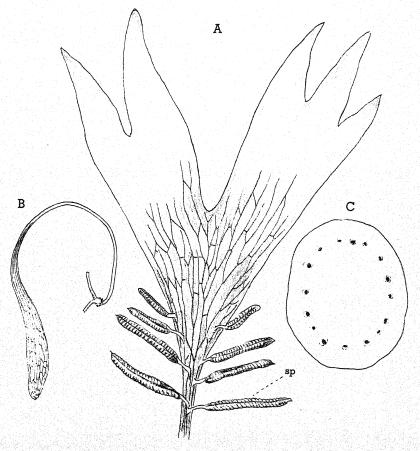


Fig. 159.—A, leaf of Ophioglossum (Cheiroglossa) palmatum, with several marginal sporangiophores; B, young plant of the same with sterile leaf; C, cross section of petiole of mature leaf (A, after Bower).

sporangium, which opens by a transverse cleft through which the spores are discharged. In some of the smaller forms of Euophioglossum the spike may be less than a centimeter in length, while in O. pendulum it may be 10 to 15 centimeters long and more than a centimeter wide. The spike in O. pendulum is more flattened than in Euophioglossum and there are relatively fewer stomata. The development of the sporangium has been studied in detail in several species, especially by Bower. According to his investigations the young spike has a band of uniform meristematic tissue occupying the margins of the flattened sporangiophore. This band of tissue becomes differentiated into alternate fertile and sterile areas, suggesting somewhat the condition in the sporophyte of the Anthocerotes. Each fertile area marks the position of a future sporangium. In the sporangial areas periclinal walls are formed by which an inner mass of tissue, the archesporium, is separated from the outer cells which form the sporangium wall. Whether or not all of the sporogenous cells of a sporangium can be traced to the division of a single archesporial cell is not certain. The outer cells of the sporogenous tissue are sterile and constitute the tapetum which finally is disorganized, the cell contents forming a sort of plasmodium containing the free nuclei of the cells. The spore mother cells separate and are embedded in this plasmodium, which doubtless contributes to their further development. When the spores are ripe, the outer cells of the sporangium lose some of their water and the resulting shrinkage causes the opening of the cleft and the discharge of the spores. There is no special mechanism like the annulus of the more specialized ferns.

The gametophyte.—The gametophyte of Ophioglossum, like that of the Psilotaceae and most species of Lycopodium, is a subterranean structure destitute of chlorophyll. In O. moluccanum it is a slender cylindrical body, a centimeter or less in length. There is a slight tuberous enlargement at the base, the upper portion being more slender. Short rhizoids are scattered over the surface. Very much like O. moluccanum is O. pedunculosum which has been considered as a synonym of that species. The gametophytes of O. pedunculosum, figured by Mettenius, are decidedly larger than those collected by the writer at Buitenzorg in Java, where several obviously different species, all referred to O. moluccanum, were growing. Mettenius found that the gametophytes of O. pedunculosum, when exposed to the light, developed chlorophyll. O. vulgatum, described by Bruchmann, has larger and more branched gametophytes and also may develop chlorophyll under the influence of light.

The gametophyte of O. pendulum is much larger than that in the other species and branches freely. It may live for many years, and multiplies by the detachment of short branches. Experiments with this species, exposing them to light, failed to show any formation of chlorophyll.

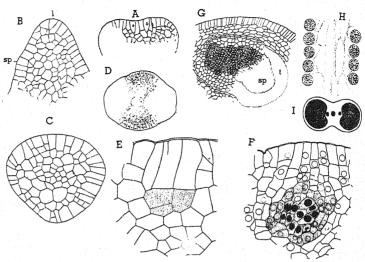


Fig. 160.—A, young sporophyll of O. moluccanum, showing dichotomy of apex; B, very young leaf, with sporangiophore, sp, and lamina, l; C, cross section of young sporangiophore; D, somewhat older stage, the shaded areas mark the sporangeogenic region; E-H, development of the sporangium in O. pendulum; I, section of mature sporangia of the same.

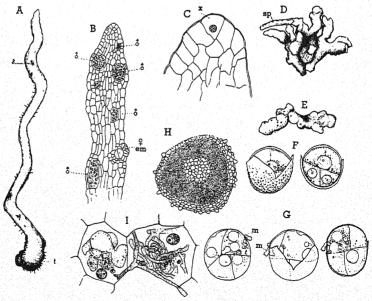


Fig. 161.—A, gametophyte of Ophioglossum moluccanum; B, section of the gametophyte: \mathcal{C} , antheridia, \mathcal{D} , archegonium with young embryo; C, apical cell of gametophyte; D, E, gametophytes of O. pendulum; F, G, germinating spores of O. pendulum; m, mycorrhizal fungus; H, section of gametophyte, showing mycorrhizal region; I, cells containing mycorrhizal fungus.

The growth is due to the activity of a definite apical cell. The gametangia form in acropetal succession and are produced on all sides of the cylindrical body or its branches. The growing tips are composed of thinwalled colorless cells containing starch and a conspicuous nucleus. In the older tissues there is always present an endophytic mycorrhiza, as in the Psilotaceae and Lycopodium. The infection occurs when the gametophyte consists of only a few cells, and unless this takes place it soon perishes. There may be secondary infections later through the rhizoids. As the endophyte penetrates the cells of the host, it forms a coiled mass of filaments and evidently consumes the starch and presumably other parts of the cell contents. The nucleus of the cell, however, remains intact; and later the fungus itself appears to be destroyed by the host cell and presumably furnishes food for the host. This symbiotic relation might be termed a reciprocal parasitism.

Antheridium.—The development of the antheridium in Ophioglossum is much like that of Equisetum. It arises from a superficial cell near the apex of the branch, which divides into a cover cell and an inner cell from which the mass of spermatocytes is derived. There are several divisions in the cover cell, the last ones forming a triangular opercular cell like that

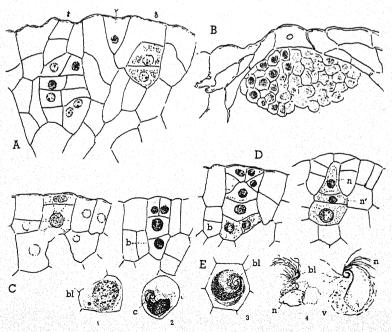


Fig. 162.—A, B, antheridia, C, D, archegonia of Ophioglossum pendulum; E, spermatogenesis. E, O. moluccanum, the others O. pendulum; bl, blepharoplast; n, nucleus.

in Equisetum and Lycopodium. The number of spermatocytes may be very large—sometimes several thousand in O. pendulum. The spermatozoids are very large and closely resemble those of Equisetum. The blepharoplast is a slender, spirally coiled filament, from which the numerous cilia are developed. The formation of the blepharoplast, by the union of a series of granules, found by Sharp in Equisetum, was not seen in Ophioglossum.

Archegonium.—The young archegonia are found near the apex of the branch, and the earliest stages are hardly distinguishable from the very young antheridia. As in these, the first division separates a cover cell from an inner one. The cover cell divides into four equal quadrant cells, giving rise to the four cell rows of the neck, which is shorter than in Equisetum; and the terminal cells are not elongated. The inner cell, as usual, divides into the central cell and the neck canal cell. The latter may divide into two cells, but usually the division is restricted to the nucleus. The separation of a definite ventral canal cell from the central cell is difficult to demonstrate, although it is probable that a division of the nucleus of the central cell does always take place.

The embryo.—The early stages of the embryo in Ophioglossum are still somewhat incompletely known. The first division in the zygote, sometimes at least, is transverse; but there is some variation and, as in Equisetum, the basal wall may be more or less strongly oblique.

To judge from somewhat incomplete data derived from a study of O. moluccanum, the epibasal portion forms the cotyledon, or primary leaf, while the whole of the hypobasal region is occupied by the large foot. At this stage there is a certain resemblance to the embryo of Anthoceros. The primary root originates endogenously from the central region of the embryo, near the junction of the cotyledon and root. It is not clear whether it originates in the hypobasal or the epibasal portion; but it seems more likely to originate from the former. A small group of actively growing cells marks the beginning of the root. Very soon a definite apical cell is formed and the root rapidly grows downward through the foot and, penetrating the tissues of the gametophyte, fastens the young sporophyte to the ground.

In the meantime the cotyledon has rapidly elongated, also pushing through the prothallium, and appears above ground as a delicate, long-stalked leaf with a lanceolate or an oval lamina. As the root pushes through the foot, the outer cells of the latter remain as a zone of larger cells in the equatorial region of the elongated bipolar sporophyte, which now consists of the cotyledon and root only. In its early condition the cotyledon is a conical body with a definite apical cell. Later this apical growth ceases and the leaf develops a slender petiole and expanded lamina.

The petiole merges insensibly with the base of the root and a longitudinal section shows that the tissues of the leaf base and root are continuous, and a single axial fibro-vascular bundle traverses cotyledon and root without interruption and there is no recognizable boundary between the two organs. The bipolar character of the young sporophyte and the way it penetrates the gametophyte may be compared with that of Equisetum. The further development of the young embryo has a counterpart also in E. debile.

The definitive sporophyte begins as a bud upon the primary root. This fact was noted by Mettenius in O. pedunculosum many years ago but received no further attention. This bud in O. moluccanum, like the primary root, is an endogenous structure. It originates close to the stele of the primary root and forms a small mass of active cells from which a conical body, the first leaf of the future sporophyte, is soon apparent. Close to the base of the leaf the stem apex is soon visible, but the leaf is developed

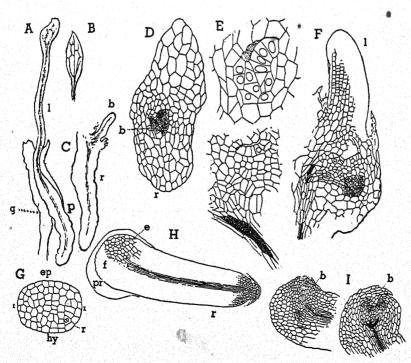


Fig. 163.—A, young sporophyte of Ophioglossum moluccanum, attached to gametophyte, consisting of the cotyledon, I, and primary root, p, only; B, lamina of a somewhat older cotyledon; C, primary root, bearing endogenous second leaf bud; D, section of embryosporophyte, showing endogenous origin of the bud; E, young endogenous bud; F, second leaf breaking through the surface of the primary root; G-I, embryo of O. vulgatum: G, young embryo, H, older embryo (G-I after Bruchmann).

independently. The axial vascular bundle in the leaf connects directly with the stele of the primary root and has no relation to the rudimentary stem apex of the young bud. The young stem apex is enclosed in a sheath formed from the leaf base and perhaps to some extent from the adjacent tissue of the primary root.

The leaf elongates rapidly and penetrates the cortex of the primary root and soon emerges, while the stem apex of the bud encased in the leaf sheath still remains within the root cortex. The first root of the young bud does not emerge until the first leaf is nearly complete. The stele of the young root joins that of the first leaf at its junction with the primary root. From this time the growth of the sporophyte is due to the activity of the stem apex, from which new leaves and roots are developed as in the adult plant.

In O. vulgatum, which has been studied by Bruchmann, the development of the embryo differs much from that of O. moluccanum. The earliest stages are not known and the relation of the organs of the older embryo to the first divisions is not clear. The young sporophyte is composed of the foot and the root, the latter being greatly developed before any definitive apical bud is established. This bud apparently is of external origin and is formed at the base of the root. The first leaf is rudimentary; the second one is functional but, according to Bruchmann, does not appear above ground until five years after it is first formed.

In O. pendulum the young sporophyte resembles that of O. vulgatum

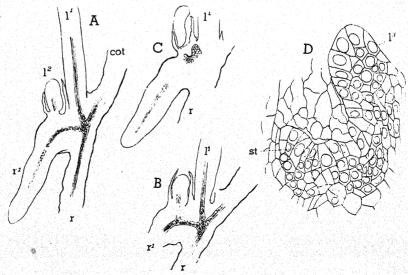


Fig. 164.—Development of the bud on the primary root of Ophioglossum moluccanum.

in the marked development of the root, associated with the prolonged subterranean habit. The hypobasal region forms a very conspicuous foot; the epibasal region may form a single massive root, as in O. vulgatum, or a root apex may arise toward one side and somewhat later a second one on the opposite side. These two roots grow out in opposite directions. The embryo reaches a large size before it emerges from the gametophyte, and the primary root may have a length of two centimeters or more without any evidence of a leaf bud being developed. The first leaf and the stem apex probably are developed from the primary root as they are in O. moluccanum. As the gametophyte of O. pendulum may live for many years, it is probable that the young sporophyte may continue its subterranean existence for an indefinite period; and it is not known just when the first leaf is developed.

In O. moluccanum the vascular bundle of the petiole of the cotyledon is collateral, the xylem on the adaxial side showing about half a dozen small tracheids. The phloem does not show any definite sieve tubes. No endodermis can be demonstrated. In the mid-region of the sporophyte there is a slight increase in the tracheary tissue. The xylem is continuous with that of the "monarch" stele of the root, which differs from that of the cotyledon in having a definite pericycle and endodermis.

About the time the first leaf of the bud emerges, a root is formed at its base and its stele joins that of the leaf at its junction with the primary root. Thus the first leaf of the bud is developed independently from tissue of the primary root of the embryo and not from the apical meristem of the young bud, which is still in a rudimentary condition.

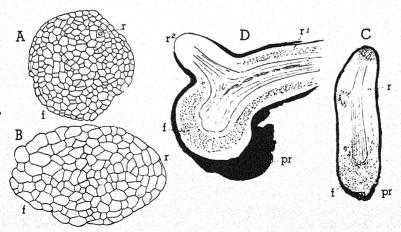


Fig. 165.—Development of the embryo of O. pendulum; A, B, C, embryos with a single primary root; D, embryo with two primary roots; f, foot; pr, gametophyte.

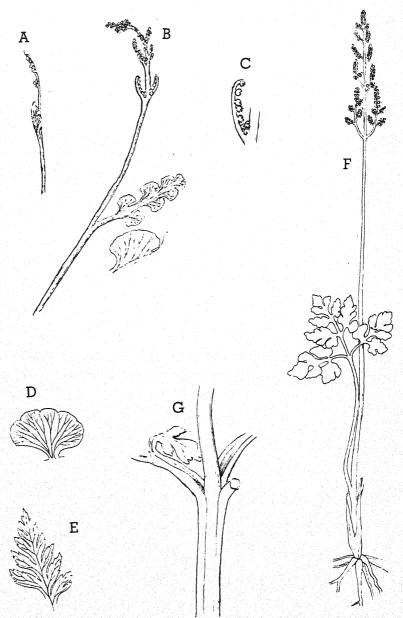


Fig. 166.—A, B, Botrychium simplex; C, sporangia of B. simplex; D, leaflet of B. Lunaria; E, leaflet of B. virginianum; F, B. ternatum; G, B. lanuginosum, base of sporangiophore fused with petiole of the leaf (F, after Luerssen).

The first leaf of the bud closely resembles the cotyledon. The second leaf is opposite the first and is enclosed with the stem apex in the basal sheath of the first leaf. The stele of the second leaf connects with that of the first root of the bud.

BOTRYCHIUM

The species of Botrychium are very variable and the number uncertain. Bitter, in his account of the genus in the Natürliche Pflanzen familien recognizes sixteen species. About half of these are found in the United States, but the total number of species is probably larger. In size they range from B. simplex, which may be only 3 to 4 centimeters in height, to B. virginianum and B. californicum, which may exceed 50 centimeters. The smaller forms of B. simplex sometimes resemble a small Ophioglossum, having an undivided sterile leaf segment and a simple sporangial spike with only a few sporangia. In all the other species both the sterile leaf segment and the sporangiophore are compound.

B. simplex and the related B. Lunaria, which represent the section Eubotrychium, have pinnately divided leaves, the fan-shaped pinnae having dichotomously branching veins radiating from the base of the leaflet. In the other species the leaves are ternately compound but the ultimate branches may show a pinnate arrangement of the leaflets. The leaflets have a definite midrib with lateral forking veins. Bitter includes all of these in the subgenus Phyllotrichum. A third section, Osmundopteris, has been proposed for B. virginianum and Lyon has made a fourth section, Sceptridium, for B. obliquum.

It is probable that Eubotrychium is the more primitive type and nearest to Ophioglossum. This is indicated both by the simpler sporangiophore and the anatomical details. The leaves have stomata on both surfaces and the mesophyll is composed of uniform tissue. Eubotrychium resembles Ophioglossum in the leaf sheath, which forms a closed hood enclosing the next younger leaf and the stem apex. The species of Eubotrychium are glabrous, like Ophioglossum, while the other species often are more or less hairy.

The rhizome is a short, upright body like that of Euophioglossum, and the leaves are in most cases spirally placed. In B. Lunaria the roots have few or no branches, like Euophioglossum; in the larger species, they branch monopodially. In B. Lunaria the peduncle of the sporangiophore joins the petiole of the leaf close to its junction with the lamina. In some other species, e.g., B. obliquum, it is free almost to the base of the petiole and might be said to be entirely independent. In B. virginianum the sporangiophore is attached close to the base of the lamina, or even above the base.

The sporangium in Eubotrychium is larger than in the other species

and is either sessile or even partially sunk, so that it suggests the condition in *Ophioglossum*. In the larger species, e.g., *B. obliquum*, the sporangia are free and may have a short pedicel. In all cases the dehiscence is by a transverse cleft, as in *Ophioglossum*.

Rhizome.—The fibro-vascular system of the rhizome is much better developed in Botrychium than in Ophioglossum. There is a massive axial cylinder with a core of pith surrounded by concentric layers of xylem and phloem and enclosed in a well-defined endodermis. In the larger species like B. virginianum, between xylem and phloem is a layer of cambium which adds internally to the wood and externally to the phloem. The re-

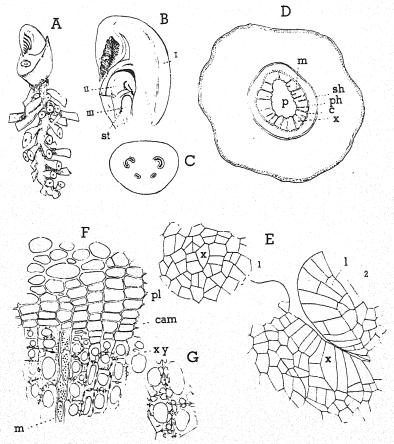


Fig. 167.—A, rhizome and terminal bud of Botrychium virginianum; B, section of the bud showing the stem apex and two leaves enclosed in the sheath of the leaf base; C, section of petiole of the leaf; D, cross section of the rhizome, showing the central pith surrounded by the woody cylinder; sh, endodermis; E, stem apex; x, apical cell; F, G, details of central cylinder of the stem.

semblance to the familiar secondary growth in the stems of conifers and dicotyledons is very close. This resemblance is increased by the development of well-marked medullary rays. The secondary thickening is much less evident and is perhaps entirely absent in *Eubotrychium*.

The wood in *B. virginianum* is composed of large prismatic tracheids with bordered pits much like those in typical coniferous wood. The medullary rays in cross section are single rows of cells extending from the pith through the entire width of the wood. The phloem contains large sieve tubes and elongated parenchyma cells. The outer part of the cortex contains some cork cells, but there is no definite periderm.

The leaf.—As in Ophioglossum, the apical bud, with the stem apex and young leaves, is enclosed in the sheath at the base of the expanded frond. This sheath in most species is a closed conical structure like that in Ophioglossum; but in B. virginianum the sheath is open on the adaxial side, forming two stipules which enclose the bud. A section of the bud toward the end of the growing season shows the frond for the next year well advanced. In Eubotrychium the young frond is straight, as it is in Ophioglossum; but in B. virginianium the lamina is bent over, concealing the young sporangiophore. Within the sheath at the base of the young frond two still younger leaves can be recognized.

While in *Eubotrychium* stomata occur on both surfaces of the leaf, and the mesophyll is uniform throughout, in the larger species, e.g., *B. lanuginosum*, stomata develop only on the abaxial surface of the lamina, and below the adaxial epidermis the mesophyll cells are more compact, although hardly forming a definite palisade tissue.

There is a single leaf trace which divides at the leaf base into two, and each of these divides again. Of the four bundles the two adaxial ones supply the sporangiophore, the abaxial one the lamina. In the larger species the bundles may divide further within the petiole, so that sometimes a section may show as many as ten. The petiole bundles are concentric like those of the typical ferns; but in *Eubotrychium* the phloem is imperfectly developed on the adaxial side of the bundle and approaches the collateral type of *Ophioglossum*.

The root.—The thick fleshy roots are developed singly from the leaf bases. In the smaller species they are usually unbranched, but in B. virginianum and other large species they may branch somewhat freely. The roots of the young sporophyte have a tetrahedral apical cell, and the root cap seems to be formed exclusively from the outer segments. In the larger roots the segmentation of the apical cell is not so regular and the lateral segments of the apical cell contribute also to the root cap. The stele of the root is diarch in B. Lunaria. In B. virginianum and B. lanuginosum it is tetrarch. There is a slight development of periderm in the larger roots,

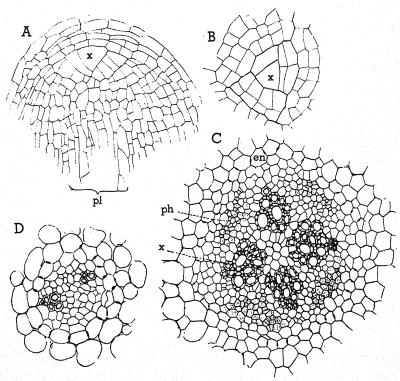


Fig. 168.—A, longitudinal, B, transverse section of root apex of B. virginianum; C, tetrarch vascular bundle of root; D, diarch root bundle of B. simplex.

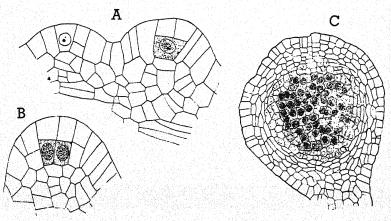


Fig. 169.—Development of the sporangium of Botrychium virginianum.

but it probably does not contribute materially to the increase in size of the roots, this being due to simple increase in the size of the cortical cells.

The sporangium.—The development of the sporangium in B. virginianum begins about a year before it is mature. The sporangium forms at the apex of the final divisions of the young sporangiophore. The young sporangium is a slightly elevated prominence, which in its earliest stage shows a large central pyramidal cell with a truncate inner face. This cell divides, as in Ophioglossum, into an outer parietal cell and an inner archesporium. Rapid cell division occurs in all parts of the young sporangium, as well as the adjacent tissue, and the sporangium becomes a globular body with a short pedicel. The archesporium divides into a large mass of sporogenous cells, surrounded by several layers of sterile wall-cells. The

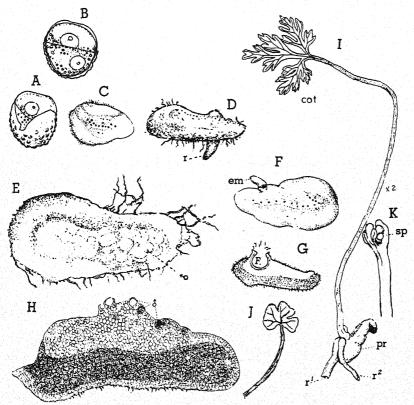


Fig. 170.—A, B, germinating spores of B. virginianum; C, D, gametophytes of B. obliquum; E, gametophyte of B. simplex; F, gametophyte of B. virginianum with embryo, em; G, section of the gametophyte of the same, showing embedded foot of the embryo; H, median longitudinal section of the gametophyte showing antheridia, c; I, gametophyte of the same, with young sporophyte; cot, cotyledon; J, cotyledon of B. obliquum; K, second leaf of B. simplex; with rudimentary sporangiophore, sp.

origin of the tapetum—whether formed in part from sterilized sporogenous tissue, as in *Ophioglossum*, or derived entirely from the inner parietal tissue—is still somewhat uncertain. The wall of the ripe sporangium is composed of 4 to 6 layers and opens by a transverse cleft, as in *Ophioglossum*.

The gametophyte.—The subterranean gametophyte of Botrychium is distinctly dorsi-ventral, thus differing from the cylindrical, radially symmetrical form in Ophioglossum. All of the species yet examined are much alike as to the gametophyte. B. obliquum will serve as an example.

The mature gametophyte in this species is a tuberous, somewhat flattened thallus, 3 to 6 millimeters in length and about half as wide. On the dorsal side is a median longitudinal ridge upon which the antheridia are borne; and numerous rhizoids, especially in the earlier stages, are found on the ventral surface. The thallus has a definite apical growth, but it is not certain that there is a single apical cell. As in *Ophioglossum* there is present an endophytic fungus which occupies a large part of the tissue but does not invade the meristematic region.

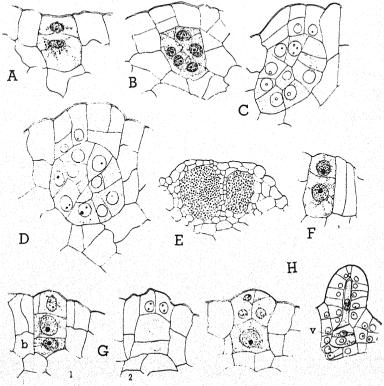


Fig. 171.—A-E, antheridia of Botrychium virginianum; F-H, archegonia of the same; v, ventral canal cell (H, after Jeffrey).

The antheridia, which closely resemble those of Ophioglossum, occupy the dorsal ridge and develop earlier than the archegonia, which form a row on either side of the antheridial ridge. The cover cells of the antheridium form a double layer in Botrychium except for the opercular cell, differing thus from Ophioglossum, where the free wall of the antheridium has a single layer of cells. The spermatozoids resemble those of Ophioglossum but are somewhat smaller, and the nucleus is more elongated, thus recalling the spermatozoids of the typical ferns.

The early stages of the archegonium differ little from Ophioglossum, but the neck is longer. There are two nuclei in the neck canal cell. As in Ophioglossum, the presence of a ventral canal cell is difficult to demonstrate; but in several cases a small nucleus was observed in the central cell, indicating that it represented the ventral canal cell.

The embryo.—There is a good deal of difference in the embryos of different species of Botrychium. In B. Lunaria, the first species to be critically studied, Bruchmann states that the young sporophyte consists of little more than a massive foot and the primary root. The cotyledon is reduced to an insignificant scale, and several similar rudimentary leaves are formed be-

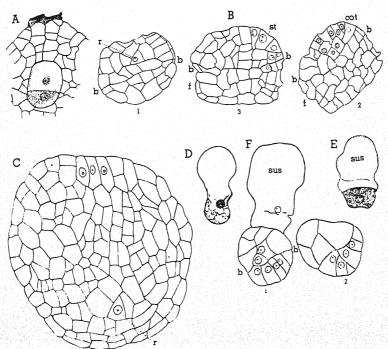


Fig. 172.—A, B, development of the embryo of Botrychium virginianum; st, stem; cot, cotyledon; r, root; C, older embryo of B. simplex; D-F, embryos of B. obliquum; sus, suspensor.

fore the first green leaf, which bears a sporangiophore, appears above ground, several years after the embryo is first formed. B. simplex has a similar embryo, but its cotyledon is better developed and the second leaf, with a rudimentary sporangiophore, emerges above ground. The development of the bud is slow compared with that of the root system. The second root develops while the cotyledon is still very small, and a third root is well advanced before any considerable growth takes place in the bud.

The early divisions in the embryo of B. simplex are variable, and it is not certain just what are the relations of the organs of the young sporophyte to these early divisions. Probably the foot and the root are of hypobasal origin, the cotyledon and stem apex of epibasal. The growth of the primary root is rapid, and there is a marked resemblance to the corresponding condition in B. Lunaria; but the cotyledon and stem apex are better developed. The primary vascular bundle extends from the cotyledon into the root. As new roots are formed their steles unite in the central region of the embryo where they are joined by the cotyledonary bundle. The latter is wanting in the rudimentary cotyledon of B. Lunaria.

Near the base of the primary root the stele has two xylems, one smaller than the other, perhaps belonging to the cotyledon; but near the apex of the root only one xylem is present, i.e., the primary root is monarch as in *Ophioglossum*. The second root is diarch.

The relations of the fertile and sterile segments of the first sporophyll have not been investigated; but it is probable that there is a very early dichotomy of the leaf fundament, like that in the later sporophylls of Ophioglossum moluccanum. Bruchmann reports that this is the case in B. Lunaria. While the embryo of B. simplex agrees in the main with B. Lunaria, the subordination of foliar structures to the roots in its young sporophyte is less marked.

The second type of embryo, that of B. obliquum, differs greatly from the Lunaria type. Lyon first called attention to the presence of a conspicuous suspensor in this species. The unicellular embryo elongates and grows downward, pushing its way into the adjacent prothallial tissue. Sometimes its course is more or less oblique. The terminal region contains most of the protoplasmic contents and is cut off from the large basal cell, which becomes the suspensor, by a transverse wall. From this terminal cell the embryo proper is developed. The first (basal) wall in the embryo cell varies somewhat in position. The next stages recall the embryo of Danaea, where there is also a suspensor. The hypobasal region (next the suspensor) develops into a large foot and from the terminal (epibasal) region the cotyledon and stem apex are formed. The young embryo is an oval body composed of the large hypobasal foot and an apical region in which there is developed a meristematic tissue from which the cotyledon and the stem apex are formed. The major part of the epibasal portion of

the embryo belongs to the cotyledon, which soon begins active growth. The stem apex at this time consists of a small group of superficial cells close to the base of the cotyledon. One of these cells becomes the apical cell of the stem. Somewhat later, at a point near the center of the embryo, a small group of actively growing cells is developed, one of these being the apical cell of the primary root, which later penetrates the foot, as in Ophioglossum moluccanum and the Marattiaceae. The root rapidly elongates, keeping pace with the similar growth in the cotyledon, so that the young sporophyte has a definite bipolar structure. It differs, however, from Ophioglossum in having the stem apex formed directly from the embryo and not secondarily from the root. A primary vascular bundle extends without interruption through the cotyledon and primary root and has no connection with the stem apex.

As the cotyledon grows it develops a massive sheath at the base, enclosing the stem apex and the second leaf. The apex of the cotyledon is bent forward, finally develops a lamina, and appears above ground as a long-stalked ternate leaf. The venation is dichotomous and the ternate form results from unequal dichotomy. The vascular strand of the second leaf is formed very early and joins the primary axial bundle of the young sporophyte.

The embryo of B. virginianum, like that of B. simplex, has a large root and foot, the root not being developed endogenously. There is no suspensor; but the cotyledon is even better developed than in B. obliquum, but has no sheath at the base. The cotyledon and root are not in the same plane and the young sporophyte does not show the bipolar form of B. obliquum. The vascular system, however, is derived exclusively from the bundles belonging to the leaves and roots.

A longitudinal section of the young sporophyte of B. virginianum shows a central pith extending to the stem apex, but no procambium can be traced above the base of the youngest leaf. With the growth of the sporophyte the leaf traces increase in size and fuse, so that they gradually form the solid cylindrical stelle characteristic of the mature rhizome.

The third and fourth leaves have a double trace which fuses into a single broad bundle, which, as it approaches the trace from the next leaf, joins with it into a bundle which in section is crescent-shaped. Opposite this is the trace from the second leaf, which, lower down, unites with it to form a complete ring.

The first tracheary tissue in the young stele belongs to the third leaf trace. Gradually a complete ring of primary wood is formed, and with the further growth of the sporophyte the metaxylem is developed with the radiating rows of tracheids traversed at intervals by the medullary rays. There is finally established the cambium zone, which continues to function throughout the life of the sporophyte.

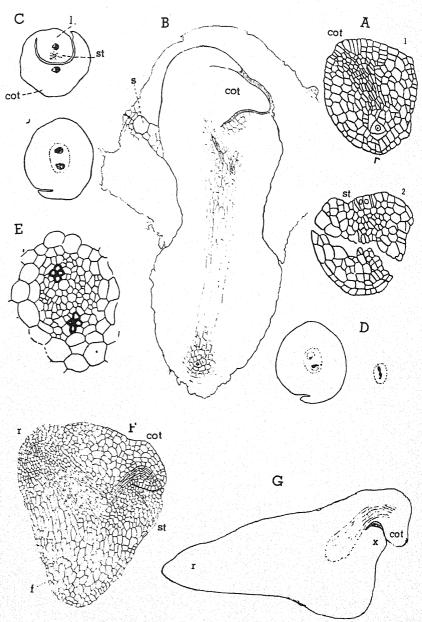


Fig. 173.—A, two sections of an advanced embryo of Botrychium obliquum: A, 1, shows cotyledon, A, 2, stem apex; B, median section of an older stage (from a photograph by Dr. H. L. Lyon); C, D, three cross sections from a series from an embryo of B. obliquum, showing union of the primary leaf traces to form the axial "stele"; E, diarch bundle of the young root; F, large embryo of B. virginianum; C, B. simplex.

HELMINTHOSTACHYS

Helminthostachys zeylanica is found throughout the Indo-Malayan regions and to north Australia. From a prostrate elongated rhizome the palmate leaves are in two rows somewhat like Ophioglossum pendulum. Some distance from the tip of the rhizome is a single expanded leaf. In front of this leaf are two younger ones, one enclosed in the stipular sheath of the expanded leaf, and the other one a simple conical body beyond which is the blunt apex of the rhizome. The leaves are less crowded than in the other genera. As a leaf breaks through the basal sheath of the next older one, the sheath splits into two stipule-like flaps, which resemble the stipules of the Marattiaceae. Thick fleshy roots, like those of Botrychium, are attached to the flanks of the rhizome. In the young sporophyte there is a single root for each leaf, but in the older plant there may be more than one.

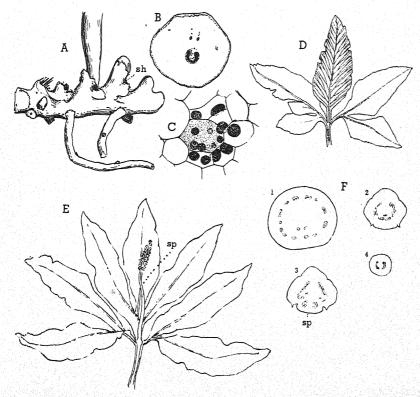


Fig. 174.—A, rhizome of Helminthostachys zeylanica; sh, stipular sheath; B, cross section of the rhizome; C, tannin sacs from the rhizome; D, leaf from young plant of Helminthostachys; E, older leaf with sporangiophore; F, sections from mature leaf: F, 1, petiole, F, 2, 3, intermediate, F, 4, peduncle of sporangiophore.

The leaf.—The leaves have a long petiole and in the young plant are ternately divided, and this is more or less evident in the palmately divided leaf of the older plant, where the secondary divisions indicate an unequal dichotomy. In texture the leaves are firmer and more leathery than in most Ophioglossaceae and the conspicuous midribs and dichotomously branched veins of the segments are like those in Marattiaceae rather than Botrychium. The peduncle of the sporangiophore is attached to the base of the lamina but it can be traced for a considerable distance below the point where it becomes free from the petiole.

Sporangiophore.—The sporangiophore of Helminthostachys is somewhat intermediate in form between Ophioglossum and Botrychium. The sporangia are densely crowded along the flanks of the spike, forming two rows as in Ophioglossum but the sporangia are in small groups, borne on short branches or secondary sporangiophores, the sporangia borne at the tips of the branches. The sporangia are sometimes more or less grown together, suggesting the synangia of the Marattiaceae. The tips of the short branches bearing the groups of sporangia sometimes expand into small leaf-like structures lying above the synangium.

Rhizome.—The anatomy of the rhizome is not very different from that of Botrychium. The stele is a hollow cylinder with narrow leaf-gaps on the dorsal side. Farmer states that there is both an internal and external endodermis and that the wood is mesarch, metaxylem being formed on both the inner and outer side of the protoxylem.

The leaf.—The petiole of the leaf is cylindrical at the base, but higher up it becomes winged at the margin, these wings passing into the lamina. In section the petiole shows a ring of concentric bundles like those in Botrychium; but on the adaxial side, within the ring of bundles, there are two others, which belong to the sporangiophore. In the petiole there is a limited development of thick-walled, hypodermal tissue such as is common in the Marattiaceae but is usually wanting in the other genera of the Ophioglossaceae.

The structure of the lamina is more like some of the Marattiaceae than like *Botrychium*. The stomata are confined to the abaxial epidermis, and the stoma is surrounded by a series of concentrically arranged cells. There is a definite palisade tissue below the upper epidermis, while the rest of the mesophyll cells are irregular in form, with large intercellular spaces.

The root.—The roots of the young sporophyte usually show a single apical cell, as in *Botrychium*; but in the larger roots there is a condition suggesting the group of initials, characteristic of the Marattiaceae. The large roots are mostly hexarch, but there is some variation in the number of xylem masses.

The sporangium.—The sporangia of Helminthostachys on the whole

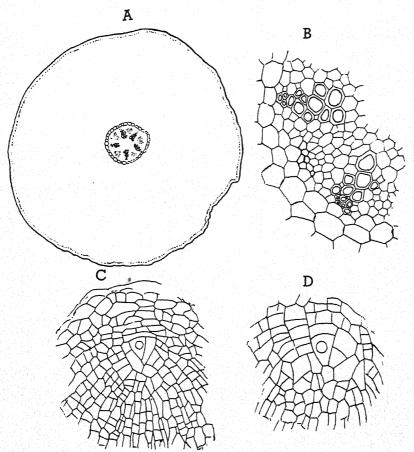


Fig. 175.—A, section of a pentarch root of Helminthostachys; B, details of the root bundle; C, root apex of Helminthostachys; D, root apex suggesting the Marattiaceous type.

resemble those of Botrychium rather than Ophioglossum. According to Bower there is formed in the young sporangiophore a sporangiogenic band of tissue much like that in Ophioglossum. The sporangiophores originate from special cell groups in the sporangiogenic band but project above the surface and later undergo a greater or less degree of branching, so that a considerable number of sporangia are formed from each secondary sporangiophore. The sporangiophores become irregularly lobed and the final divisions become the sporangia, very much as in Botrychium; but the individual sporangia are less distinct. The sporogenous tissue increases in size and several layers of the surrounding tissue form a very thick tapetum, the cells of which break down and serve to nourish the developing spores.

The sporangia are often united in groups, remotely suggesting the synangia of the Marattiaceae.

The gametophyte.—The gametophyte of Helminthostachys is a subterranean, somewhat irregular structure consisting of a basal tuberous portion and an upright cylindrical body upon which the gametangia are borne. Except that it is thicker and relatively shorter, it may be compared with that of Ophioglossum moluccanum. Archegonia and antheridia resemble those of Botrychium rather than Ophioglossum. The gametophyte is monoecious, but sometimes there is a tendency toward a unisexual condition. Like the other members of the order, there is always an endophytic mycorrhiza present.

The embryo.—The early stages of the embryo are imperfectly known but resemble those of Botrychium rather than Ophioglossum. Lang found a suspensor present, as in Botrychium obliquum. The cotyledon is rudi-

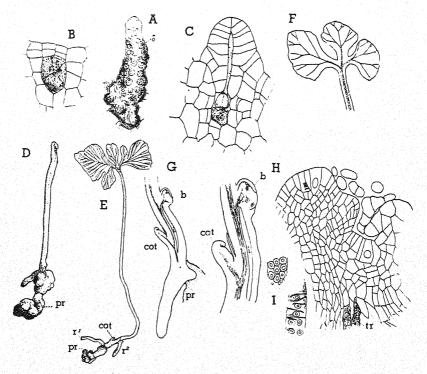


Fig. 176.—A, gametophyte of Helminthostachys; B, antheridium; C, archegonium; D, gametophyte, pr, with young sporophyte attached; E, an older stage; cot, the rudimentary cotyledon; F, first functional leaf; G, sections of young sporophyte showing the cotyledon and the bud, b, from which the axis is developed; H, apex of the bud; tr, primary tracheids; I, tracheids showing bordered pits (A, B, C, after Lang).

mentary, but the second leaf is functional and resembles the cotyledon of *Botrychium obliquum*. It has a slender petiole and ternate lamina evidently resulting from an unequal dichotomy, and the venation is dichotomous and resembles the type of *B. Lunaria*.

The young sporophyte has a conspicuous foot embedded in the gametophyte; the large primary root grows out at right angles to the foot and is continued into the axis of the sporophyte, which forms an elongated internode between the cotyledon and the second leaf. At the base of the latter is a conspicuous stipular sheath which encloses the stem apex and the third leaf. While the sheath may be absent from the base of the cotyledon, it is sometimes quite conspicuous; and the cotyledon, although apparently never functional, has the rudimentary lamina bent over as in Botrychium virginianum.

The stele of the root is continuous with that of the shoot, and forks below the insertion of the cotyledon into two unequal branches, the shorter branch belonging to the cotyledon. Whether or not in an earlier stage, before the formation of the second leaf, there is the same orientation of the steles of the primary organs of the embryo that obtains in *Botrychium* is not known. It is quite possible, in view of the greater development of the axis and terminal bud in *Helminthostachys*, that the stele of the elongated axis is in part of truly cauline origin.

In the young sporophyte tannin cells are present. These are common in the Marattiaceae but are not found in the other Ophioglossaceae.

The petiole of the second leaf contains two vascular strands: one supplying the larger lobe of the lamina; the other dividing into two, of which one goes to the terminal lobe and the other to its sister lateral lobe. Between the base of the primary root and the cotyledon there is a definite internode (hypocotyl?), and a similar internode between the cotyledon and second leaf.

The apical cell of the shoot is much like that of *Ophioglossum*, having a truncate inner face. The stele of the axis could not be traced with certainty beyond the base of the youngest leaf, and it was concluded that the axial stele is composed exclusively of coalescent leaf traces, as it is in the other Ophioglossaceae.

RELATIONSHIPS

While the three genera differ in various ways, there can be little question that they are all related closely enough to be included in a single family. *Ophioglossum* may be regarded as the most primitive type; it more resembles the hypothetical ancestors of the Filicineae than any other known form.

From the simple sporangiophore of *Ophioglossum*, with its sunken rather indefinite sporangia and the correspondingly simple sterile lamina, the transition to the decompound frond and repeatedly branched sporangium of *Botrychium* is not an abrupt one, and this is true also for the sterile leaf-lamina. The simpler species of *Botrychium*, like *B. Lunaria* and *B. simplex*, may be said, in a way, to connect *Ophioglossum* with the more specialized species of *Botrychium*, like *B. lanuginosum* and *B. virginianum*.

Helminthostachys, on the whole, is nearer to Botrychium; but in several respects, notably the character of the leaves and sporangia, it shows an approach to the Marattiaceae. Whether or not the small foliaceous structures above the "synangia" might be compared to the sporophyll of the Marattiaceae, with the synangia on the abaxial surface, is a question.

Bower recognizes the primitive character of the Ophioglossaceae as a whole but believes Botrychium and Helminthostachys are the more primi-

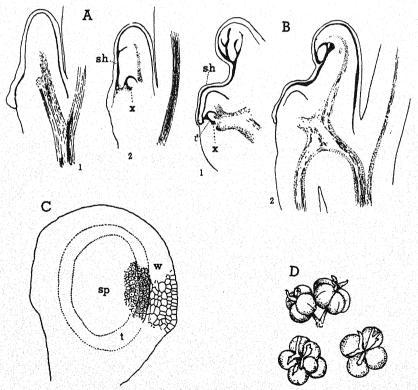


Fig. 177.—A, B, sections of the apical bud of the young sporophyte of Helminthostachys, showing the arrangement of the vascular bundles of the shoot; C, section of a young sporangium; D, sporangiophores (C, from preparation made by Professor L. L. Burlingame).

tive types and that Ophioglossum, which he considers a more specialized form, is secondary. This is hardly borne out by a study of the development of the sporophyte in Euophioglossum. Here there is no cauline stele, the "dictyostele" being a complex of united leaf traces; and the assumption that the simple sporangiophore of Ophioglossum is reduced from the more specialized condition in Botrychium is hardly consistent with the course of development of the sporangium in the two types. Bower also considers the reticulate venation of Ophioglossum as secondary. He says this type of venation is not known in any Palaeozoic ferns but is first met with in the Mesozoic. This is a point that needs further elucidation.

CHAPTER XIV

EUSPORANGIATAE: MARATTIALES; ISOETALES

The second order of the Eusporangiatae, the Marattiales, resemble the typical ferns in general habit. Both in the form of its leaves, which are coiled in the bud, and in their venation they are much like the common ferns, and as in them the sporangia are borne on the abaxial surface of the leaf. The sporangia, however, are very different, and in both structure and development show resemblances to those of the Ophioglossaceae.

The Marattiaceous type is a very old one, and these few survivors of the Palaeozoic fern flora are especially important in connection with the evolution of the Filicineae. The fleshy texture of the leaves of most of them recalls the Ophioglossaceae rather than the typical ferns. In size they range from some of the smaller species of Danaea, with leaves only a few inches in length, to some of the largest known ferns, e.g., Angiopteris evecta, of the eastern tropics, the leaves of which may reach a length of 5 to 6 meters.

The Marattiaceae for the most part are found in the tropical rainforests, where they form a very characteristic feature of the vegetation. There are probably about two hundred species, but there is some uncertainty about the species of some of the genera. This is especially true of Angiopteris, which has been described as a single variable species by some writers while others recognize in it over one hundred species.

There are known at present seven genera, all referred to the family Marattiaceae, which, however, has been divided into several sections or subgenera. The most widespread genus is Marattia, which occurs in the tropics of both hemispheres. M. Douglasii reaches Hawaii, and Angiopteris is common in the eastern tropics and extends to southern Japan and northern Australia as well as to Polynesia. Archangiopteris and Protomarattia are restricted to South China, Tonking, and Formosa, while Danaea is exclusively American, Kaulfussia (= Christensenia) has two species, the best-known, K. aesculifolia, occurring in the Indo-Malayan region. Macroglossum is known, as yet, only from Borneo and Sumatra. Of these seven genera, Kaulfussia differs most markedly from the others in the structure of its leaves and some other characters. The stem in Kaulfussia is a prostrate rhizome, not unlike that of Ophioglossum pendulum and Helminthostachys. This dorsi-ventral type is found also in some species of Danaea, although less marked there than in Kaulfussia; and a dorsi-ventral rhizome

has also been described by Hyata for Archangiopteris and Protomarattia. In most of the Marattiaceae, however, the stem is a short upright "caudex" or trunk which in Angiopteris and Marattia may be a foot or two in height and almost as thick. Much of the thickness is due to the persistent leaf bases, which completely cover the surface of the trunk.

Kaulfussia has the simplest stem structure of any of the Marattiaceae and shows the greatest resemblance to the Ophioglossaceae. In the relation of stem and leaf it has its nearest analogy in Helminthostachys; but anatomically it is more like Ophioglossum, especially O. pendulum. More than any other member of the Marattiaceae it approaches the monophyllous condition characteristic of the Ophioglossaceae, and sometimes the adult plant has only one expanded leaf.

The leaf has a long petiole, about a centimeter in diameter, which equals or exceeds in thickness the rhizome. At the base of the petiole are two conspicuous stipules, joined by a broad commissure, which extends entirely around the apex of the shoot exactly as in *Helminthostachys*. The

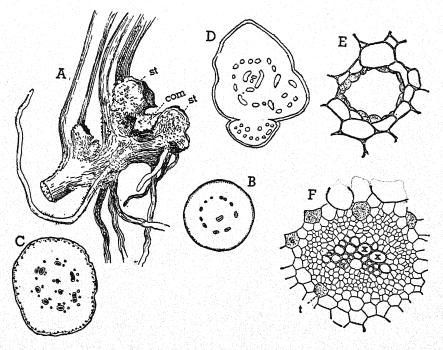


Fig. 178.—A, rhizome and leaf bases of Kaulfussia aesculifolia; st, stipules; com, cummissure; B, section of rhizome; C, section of petiole; D, section of rhizome of Danaea jamaicensis: E, mucilage duct; F, vascular bundle of petiole; x, tracheids; t, tannin sac.

anatomy of the petiole is much like that of the rhizome and closely resembles the stem structure of Ophioglossum pendulum.

The stem.—In cross section the rhizome shows a circle of about a dozen bundles, within which is a single bundle. The vascular skeleton of the rhizome was shown by Kühn to be a hollow "dictyostele" with large open meshes. This is formed by a fusion of the bundles of the petioles, which do not unite into a single leaf trace but continue directly into the stem. There are occasional anastomoses of the bundles within the petiole, so that the anatomy of the petiole and rhizome is very much the same. The arrangement of the bundles in the petiole, except for the presence of the central strand and the method of junction with the vascular system of the rhizome, is very much like that in Ophioglossum pendulum.

The ground tissue of the rhizome—and this obtains for all the Marattiaceae—is composed of simple parenchyma, also recalling the Ophioglossaceae. The outer cortical cell walls may show the cork reaction. The vascular bundles are concentric in structure like those in the petiole of Botrychium and Helminthostachys, and thus differ from the collateral bundles of Ophioglossum.

The rhizome in *Danaea* may be dorsi-ventral, as in *Kaulfussia*, e.g., *D. jamaicensis*, *D. Jenmani*; but in *D. elliptica*, a larger species, the stout upright rhizome has the leaves spirally arranged as they are in *Marattia* and *Angiopteris*.

The arrangement of the vascular bundles is much like that in *Kaulfussia*, though instead of the single central bundle there are several; but in the young sporophyte there is a single one, as in *Kaulfussia*.

The stem in the adult plant of Marattia douglasii is an almost globular, upright caudex, a foot or more in diameter. It is completely covered with the persistent fleshy bases of the very large, spirally arranged leaves. Above the base with the two large fleshy stipules there is a sort of pulvinus, where the leaf finally becomes detached, leaving a conspicuous scar marked by the broken ends of the vascular bundles. Angiopteris closely resembles Marattia in general appearance but reaches even greater dimensions.

Sections of the stem in Angiopteris show many bundles arranged in several concentric circles. These concentric circles are the sections of a series of funnel-shaped zones of anastomosing bundles. Mettenius, in his study of Angiopteris, says: "The vascular bundles form funnel-shaped zones with the lower ends in the stem, and their upper portions continued into the leaves as leaf traces. Segments of the outer zone pass into the leaves as leaf traces and the gaps thus left are filled by segments of the next inner zone."

The complicated system of concentric meshed zones in the adult stem of Angiopteris is evidently built up of the union of leaf traces which are

themselves composed of a mesh of anastomosing bundles which in the stem unite with other similar leaf traces. The structure of the adult stem in *Marattia* is probably much like that in *Angiopteris*, but details are lacking. A young specimen of *Marattia fraxinea* examined by Kühn showed two circles of bundles in the stem instead of the larger number found in *Angiopteris*. This is much more like *Danaea* than *Angiopteris*, but further investigation of the structure of the adult plant is desirable.

The single central bundle in Kaulfussia and the corresponding small group in Danaea represent bundles which belong to the stem itself and are

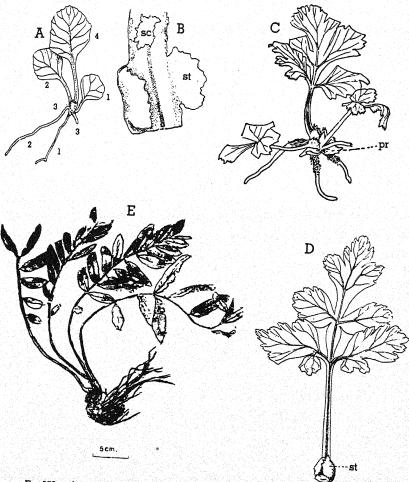


Fig 179.—A, young sporophyte of Danaea jamaicensis with three leaves; B, base of fourth leaf; st, stipule; sc, scale; C, young sporophyte of Marattia Douglasii; D, older leaf of the same; E, mature sporophyte of Danaea Jenmani.

independent of the leaf traces. These cauline bundles occur in all the Marattiaceae, and are not known in any of the Ophioglossaceae. They are known as "commissural" bundles.

In the stem of the young sporophyte a single apical cell can be demonstrated; but whether or not this is true also for the full-grown sporophyte is doubtful.

Mucilage ducts.—A marked feature of the Marattiaceae is the presence of conspicuous mucilage ducts. In Danaea these are especially well developed. A section of the rhizome shows a ring of these in the outer cortex and a second group in the central region associated with the axial group of vascular bundles. A study of the earlier stages shows that they most commonly originate from the fusion of a row of cells. Such ducts are "lysigenous." It is possible that "schizogenous" ducts may also occur, i.e., ones in which the cavity of the duct is an intercellular space containing mucilage secreted by the surrounding cells; but this is doubtful. In all the Marattiaceae are found cells containing tannin, such as are found in Helminthostachys but not in the other Ophioglossaceae. There is also a development of mechanical tissue—sclerenchyma or collenchyma—the former especially developed in the petioles of the large leaves of Angiopteris, Marattia, and Danaea. This is replaced by collenchyma in the leaflets and is the only mechanical tissue in Kaulfussia.

The leaf.—The leaf in the Marattiaceae ranges from the undivided lanceolate leaf of Danaea simplicifolia to the gigantic decompound leaves of Marattia and Angiopteris. Most of the species of Danaea, also Archangiopteris and Macroglossum, have simply pinnate leaves, which in Macroglossum Alidae may be four meters long. In Kaulfussia the leaves are palmately divided into three to seven leaflets, the longer leaves looking curiously like the leaf of the horse chestnut—hence the specific name "aesculifolia." The ternate form also recurs in the early leaves of the other genera and is sometimes retained in quite large leaves of Marattia. This recurrence of the ternate leaf form recalls Helminthostachys and the ternate species of Botrychium. The leaves are usually smooth; but in the earlier stages there may be a sparse development of hairs and scales.

The conspicuous fleshy stipules of the leaf base are characteristic and, as already indicated, remain attached to the caudex after the leaves fall away. The pulvinus marking the point of detachment also may be formed in the smaller divisions of the leaf, the leaflets sometimes separating from the main or secondary rachis in the same way as the petiole breaks away from the leaf base. The stipules are joined by a broad "commissure," which in Kaulfussia forms a sheath enclosing the apical bud, closely resembling the corresponding stage in Helminthostachys.

The cotyledon is fan-shaped with dichotomous venation in most cases.

Kaulfussia differs from the other genera having the venation reticulate, closely resembling that of Ophioglossum. The development of a midrib is secondary.

The young leaf is coiled like that of the typical ferns, and in general the venation is decidedly fern-like, the final branching being dichotomous. This type of venation is also found in *Helminthostachys* and some species of *Botrychium*.

The petiole of the leaf shows much the same structure as the stem, except that there is a hypodermal zone of mechanical tissue—sclerenchyma or collenchyma. The simplest leaf structure is found in Kaulfussia, which most nearly resembles Ophioglossum. This is true not only in the venation of the leaf but also in the anatomy of the lamina. In the early leaves the lamina has but three layers of quite uniform mesophyll, exactly like Euophioglossum. In the mature leaf the mesophyll is more compact but there is no true palisade tissue. Stomata are present only on the abaxial surface of the leaf, and the stoma-pores are greatly enlarged. The structure of the lamina is much the same in all of the Marattiaceae and resembles that in Helminthostachys. The primary leaf stalk and the secondary branches of the frond often show swellings or nodules, which are especially conspicuous in some species of Danaea. The leaflets have a conspicuous midrib, and

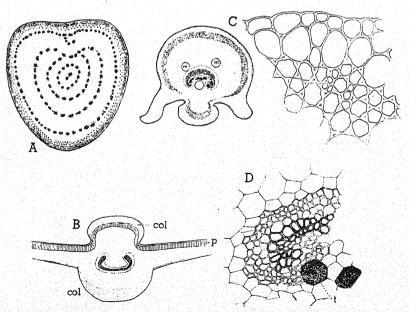


Fig. 180.—A, section of petiole of Angiopteris; B, section of a pinna; col, collenchyma; C, collenchyma cells from rachis of Marattia alata; m, mucilage ducts; D, vascular bundle of rachis of Marattia alata.

the lateral veins are forked, the branches extending to the margin of the leaflet. There is a conspicuous palisade tissue, below which is the characteristic spongy mesophyll with large intercellular spaces. The stomata are confined to the abaxial surface, and in Danaea the stoma is surrounded by a series of narrow cells, much as in Helminthostachys. Danaea trichomanioides has delicate membranaceous leaves, which would probably show a much simpler structure.

The root.—The roots in the Marattiaceae are thick and fleshy, like those of the Ophioglossaceae. In the smaller forms, like Danaea, the roots originate from the leaf base. In Danaea two at least belong to each leaf. In Angiopteris, with its massive caudex, the roots originate from the inner zones of vascular bundles and must penetrate a large amount of tissue before they emerge from the caudex. In Kaulfussia the roots are un-

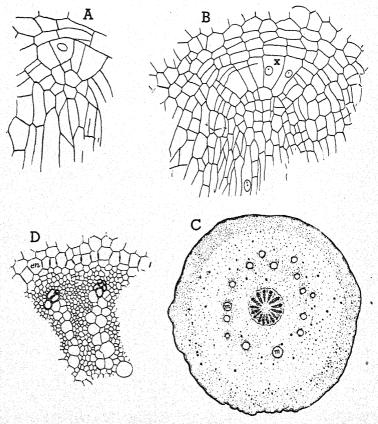


Fig. 181.—A, apex of primary root of Angiopteris; B, apex of small root of Danaea jamaicensis; C, section of large root of Angiopteris; m, mucilage ducts; D, details of the vascular cylinder of the same; en, endodermis.

branched, like those of *Euophioglossum*; and in *Angiopteris* and *Marattia* branching is not frequent. In the former a dichotomy has been noted by Miss Shove, a condition also occasionally found in *Euophioglossum*. *Danaea* differs markedly from the other genera in that its roots branch freely, thus resembling *Botrychium* and *Helminthostachys*.

The roots of the very young sporophyte show a single apical cell, but this is replaced in the later roots by a group of similar initial cells. The primary root in all the forms that have been investigated is diarch; but in the roots of the mature sporophyte the stele shows a larger number of xylems. The root from a large specimen of Angiopteris may be five millimeters or more in diameter. A cross section of a large root of Danaea elliptica showed an outer zone of brown (probably cork) cells, within which was a zone about three cells thick of sclerenchyma; the bulk of the root was composed of parenchyma. A conspicuous endodermis enclosed the stele, which showed twelve xylem rays, alternating with as many phloems. The center of the stele was occupied by the pith. In the ground tissue outside the endodermis was a ring of conspicuous mucilage ducts. In the smaller species the number of xylem rays is less and the sclerenchyma is much less evident; and in Kaulfussia only four xylem rays were found in most cases. In the large roots of Angiopteris the number of xylem rays is even greater than in Danaea. Root hairs are found upon the younger parts of the root but are not conspicuous. These are multicellular in Danaea and Kaulfussia, and West reports them in other Marattiaceae.

An endophytic fungus is usually found in the primary root of all the Marattiaceae but is generally absent from the large roots of the adult sporophyte. West has described it as a definite species, *Stigeosporium Marattiacearum*.

The sporangium.—Unlike the Ophioglossaceae the Marattiaceae have no sporangiophore but the sporangia are borne on the abaxial surface of normal leaves. These sporophylls in most cases differ neither in size nor structure from the sterile leaves. In Danaea, however, the sporophylls are decidedly contracted and the large synangia almost completely cover the lower surface of the pinnae. In Angiopteris and the related genera Archangiopteris and Macroglossum there are distinct sporangia which form a compact "sorus," but in Kaulfussia, Marattia, and Danaea they form a solid synangium in which the separate masses of sporogenous tissue are developed very much as in Ophioglossum.

The sorus, or synangium, is not protected by an indusium, such as is found in most typical ferns (Leptosporangiatae), although around the synangium are often a few hairs or scales which might be interpreted as an indusium. In *Danaea* the elongated synangium is sunk in a groove formed by ridges which separate the adjacent synangia. The summit of these

ridges is expanded into a flange which extends over the adjacent synangia, leaving only a small part of the upper surface of the synangia exposed. Whether or not this should be considered as an indusium is questionable. A similar condition, but less developed, is found in *Macroglossum*.

The development of the synangium begins when the sporophyll is still very small. Over a vein a cushion of tissue projects above the leaf surface. Bower states that in *Danaea* there is a somewhat indefinite segregation of fertile and sterile areas, as in *Ophioglossum*, and that two rows of sporoge-

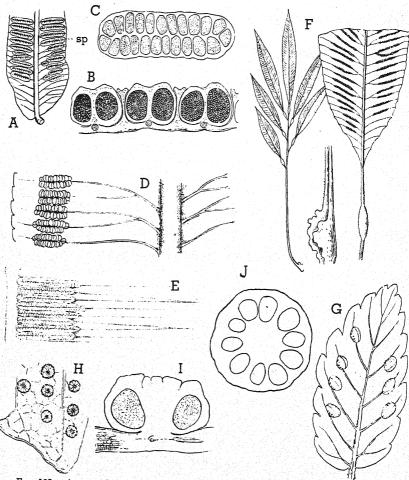


Fig. 182.—A, sporophyll of Danaea, with elongated synangia; B, cross section of three synangia of D. jamaicensis; C, horizontal section of a synangium; D, sori of Angiopteris; E, sori of Macroglossum Alidae; F, Archangiopteris Henrye; G, synangia of Marattia Douglasii; H, synangia of Kaulfussia; I, vertical, I, horizontal sections of synangium (F, after Christ and Giesenhagen).

nous cell masses, not very sharply defined, are separated by bands of sterile cells. In *Marattia* there is a deep longitudinal median cleft which divides the synangium into two parts. In *Danaea* no such cleft is formed. In *Danaea*, also, the individual spore masses or "loculi" are less clearly defined than in *Marattia*. The further development is much like that of the sporangia of *Botrychium* and *Helminthostachys*.

In Kaulfussia the young synangium is a circular or oval cushion and the loculi are arranged in a ring. In Danaea and Kaulfussia no special mechanical apparatus is developed and the dehiscence is effected by a shrinkage of the tissue surrounding the slit by which each loculus opens.

In Marattia the young synangium consists of two parallel ridges, which increase in height and meet above the median cleft, which is not visible in the mature synangium. In each half of the synangium the development proceeds much as in Danaea. When ripe, the outer tissue of the synangium

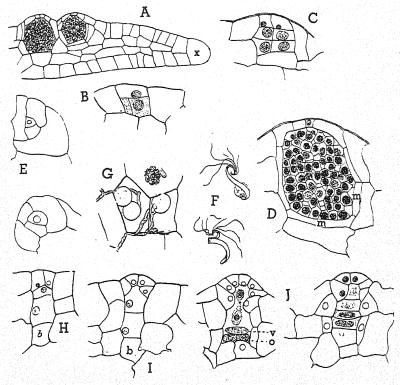


Fig. 183.—A, longitudinal section of gametophyte of Kaulfussia, showing apical cell and antheridias; B-D, development of antheridium of Kaulfussia; E, surface view of antheridium showing the opercular cell; F, spermatozoids of Marattia Douglasii; G, prothallial cells containing mycorrhiza; H-J, development of archegonium in Angiopteris; v, ventral canal cell; o, egg.

contracts and causes the two halves to separate like the leaves of a book, and each loculus opens by a slit on the inner side.

The synangium of Marattia is intermediate in structure between the solid synangium of Danaea and the separate sporangia of Angiopteris and Macroglossum. The sorus of Angiopteris in its earliest condition resembles closely the synangium of Marattia. The development begins at a much later period than in Marattia, but very soon the individual sporangia become evident and the further development proceeds much as in Botrychium. Probably the archesporium can be traced back to a single hypodermal cell from which the mass of sporogenous cells develops. Surrounding the sporogenous tissue is the tapetum, the cells of which remain intact until the division of the spores is complete, and Bower found that this condition is true for the other genera also. The wall of the sporangium is thicker on the outer side, and near the apex is a transverse band of cells with thickened walls which by their contraction cause the sporangium to open by a vertical slit on its inner face. The rudimentary "annulus" is much like that in the sporangium of the Osmundaceae, a family of ferns intermediate between the Eusporangiatae and Leptosporangiatae.

Undoubtedly related to Angiopteris, but having a somewhat less-specialized sporangium, is Macroglossum, which suggests an intermediate position between Angiopteris and Danaea. Here the elongated sori are sunk in a groove, as in Danaea.

Which type, the free sporangium or the synangium, is the more primitive it is impossible to say, as both, so far as is known, are of about equal antiquity. Considering the intermediate condition in *Marattia* and *Macroglossum*, it would appear that the free sporangia were secondary, the synangium being the more primitive condition.

The gametophyte.—Unlike the Ophioglossaceae, the gametophyte in the Marattiaceae is a green fleshy thallus closely resembling such a liverwort as Aneura or Anthoceros.

The spores of the Marattiaceae are small and contain no chlorophyll, but the contents include oil, starch, and albuminous granules. The germination has been studied by Luerssen and Jonkmann in species of *Marattia* and *Angiopteris*, and probably is much the same in the other genera.

The outer membrane of the germinating spore is ruptured and the spore becomes many times its original size before any cell division occurs, which takes place a month or more after germination begins. In the meantime chlorophyll has developed and the undivided cell contains numerous conspicuous chloroplasts. The first wall divides the cell into nearly equal parts, one of which may form a rhizoid; but this is not always the case.

As the gametophyte grows it becomes a broad thallus with a definite growing point and dorsi-ventral structure. From the ventral surface

numerous rhizoids are formed. In Danaea these are multicellular, like the root hairs of the sporophyte. The gametophyte may reach a considerable size, sometimes two or three centimeters in length, and is much more massive than that of the common ferns and more like a liverwort. The gametophyte may live for a long time. The writer has kept prothallia of Marattia Douglasii in the laboratory for over a year, during which time they grew vigorously. The older gametophytes may branch dichotomously or by forming lateral shoots, which sometimes become detached and develop independent plants.

The gametophyte is thicker in the median region, which forms a sort of midrib projecting strongly on the ventral side and back of the growing point, developing a cushion upon which the archegonia are borne. The midrib merges into the wings of the thallus, which consist of several layers of cells instead of the single cell layer found in the typical ferns. Although the gametophytes in *Danaea* may reach a relatively large size, the wings at

the margin may be only a single cell in thickness.

The midrib begins to form at an early period and may have a thickness of 8 to 10 cells. As a rule antheridia are formed first on the lower surface of the midrib or near it; later, nearer the apex and confined to the cushion-like enlargement of the midrib, the archegonia are developed. There is sometimes a tendency to dioecism in the gametophytes, which may bear gametes of only one sex.

An endophytic mycorrhiza much like that in the gametophyte of the

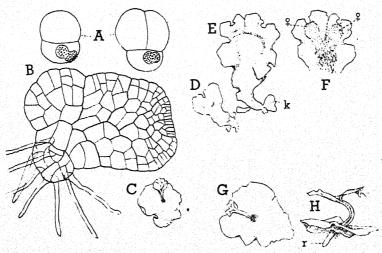


Fig. 184.—A, germinating spores of Marattia frazinea; B, young gametophyte of the same; D, young gametophyte of Marattia Douglasii; E, F, the same a year later; C, G, H, prothallia with young sporophyte (A, B, after Jonkmann).

Ophioglossaceae is almost always present in the central tissues of the gametophyte. To what extent there is a symbiotic relation between the host and the endophyte is not clear; but it is probable that the endophyte in this green prothallium is more nearly a true parasite than in the saprophytic gametophyte of *Ophioglossum*.

The gametangia.—The antheridium is very much like that of Ophioglossum, and the early divisions show much the same variations. In none of the species investigated were the spermatozoids as numerous as in some of the Ophioglossaceae. Kaulfussia, in the size of both the antheridium and the spermatozoids, is most like Ophioglossum. In the details of spermatogenesis it agrees closely with Ophioglossum, and in both form and size

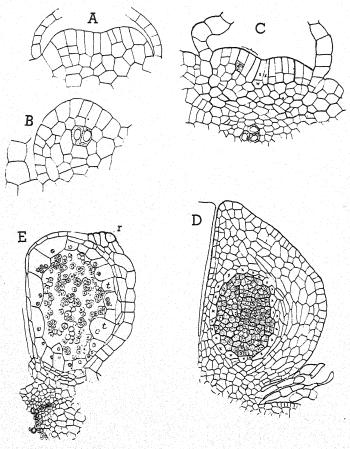


Fig. 185.—A, B, early stages of the sporangium of Angiopteris; C, transverse section of young synangium of Marattia fraxinea; D, older synangium of the same; x, tapetal cells; E, older sporangium of Angiopteris; t, tapetum (A, B, after Goebel; C, D, after Bower).

of the spermatozoids Kaulfussia more nearly resembles Ophioglossum than it does the other Marattiaceae.

The archegonium also is much like that of Ophioglossum, but the neck is even shorter. The archegonia usually arise in acropetal succession from the cushion at the apex of the prothallium. The neck canal cell is very broad; it may divide into two cells, but usually the division is confined to the nucleus. Except in Danaea a large ventral canal cell is present; but in Danaea, as in Ophioglossum, the presence of a ventral canal cell is difficult to prove. The four rows of neck cells remain short, with only three or four cells in each row, and the neck projects but little.

The embryo .- There is somewhat the same variation in the development of the embryo of the Marattiaceae as is found in the Ophioglossaceae. In all of the species investigated the first (basal) wall is transverse and there may be a regular quadrant division; but sometimes, e.g., in Danaea jamaicensis, the hypobasal cell develops into a suspensor like that of Botrychium obliquum. In Macroglossum there is a conspicuous suspensor, but its origin is not known. Land also reported the occasional development of a suspensor in Angiopteris.

Usually in Angiopteris, Marattia, and Kaulfussia the basal wall divides the embryo into two equal parts. From the hypobasal cell, next the archegonium neck, the foot is developed, from the epibasal, the cotyledon and,

later, the stem apex.

The young embryo is somewhat flattened at first, but soon becomes nearly globular or pear-shaped and subsequently elongated vertically. At this stage the embryo is bipolar like that of Ophioglossum moluccanum.

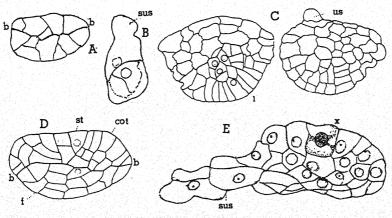


Fig. 186.—A, young embryo of Kauljussia; b, basal wall; B, young embryo of Danaea jamaicensis; sus, suspensor; C, section of older embryo of same species; D, embryo of Angiopteris; E, embryo of Macroglossum, with large suspensor.

The primary root is formed only after the embryo has attained considerable size. It is first recognizable as a group of actively dividing cells near the center of the embryo, which soon develop the growing point of the young root exactly as in *Ophioglossum moluccanum*. The single apical cell is somewhat variable in form. The root grows downward through the foot, which is no longer recognizable and emerges on the lower side of the gametophyte.

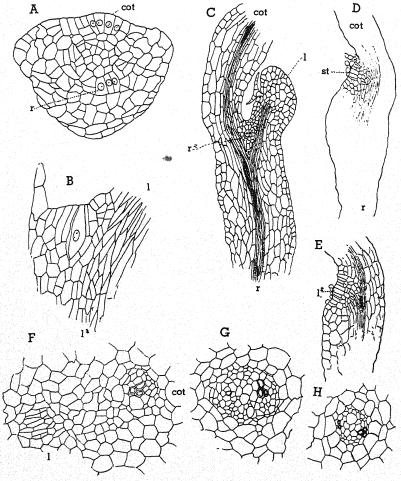


Fig. 187.—A, embryo of Danaea elliptica; cot, cotyledon; r, root; B, stem apex of young sporophyte of D. elliptica; C, nearly median section of young sporophyte of the same; cot, cotyledon; l, second leaf; r, primary root; r, second root; D, E, sections of young sporophyte of Angiopteris; st, stem apex; l, second leaf; F, G, two of a series of transverse sections of a young sporophyte of Danaea jamaicensis, showing union of leaf traces to form the axial bundle of the stem; H, vascular bundle of the primary root.

The cotyledon develops from the epibasal region and grows rapidly upward almost in a line with the root. The cotyledon comprises the major part of the epibasal tissue, but close to its base there appears an inconspicuous prominence, the future stem apex. This has a single apical cell, either three- or four-sided, often with a truncate base like that of Ophioglossum. The cotyledon grows rapidly, piercing the dorsal tissue of the gametophyte and emerging on the upper side. At this stage it may be compared with that of Ophioglossum moluccanum except for the presence of the stem apex, which, however, is very inconspicuous.

As in Ophioglossum the primary vascular bundle is a continuous strand traversing the cotyledon and root, and there is no development of stelar tissue in the stem region. In Danaea the primary vascular strand is collateral, as it is in Ophioglossum; but in the other Marattiaceae it is concentric, although the phloem is less developed on the inner side and the

bundle may thus approach the collateral structure.

The young cotyledon is bent over the stem apex, much as in Botry-chium. The apex broadens and develops the lamina. This is followed in most cases by a dichotomy, which is repeated, and the lamina becomes fanshaped with strictly dichotomous venation. In Angiopteris and Macroglossum there is sometimes a suggestion of a midrib in the cotyledon, but this may be due to an unequal dichotomy early in the development. This condition is sometimes seen also in Danaea. In Kaulfussia the spatulate cotyledon has reticulate venation closely resembling the cotyledon of Ophioglossum moluccanum.

As the second leaf develops, its axial vascular strand is continued downward to form the second leaf trace and unites with the primary bundle and thus inaugurates the vascular system of the axis of the young sporophyte. No stelar tissue is developed in the axis above the junction of the first

leaf traces.

The development of the vascular system in the young sporophyte is essentially the same in all the genera that have been critically studied. It is most easily traced in the simpler forms like Kaulfussia and Danaea. In the latter, as already indicated, the vascular system begins as a simple axial strand which is continuous through the cotyledon and primary root. The bundle in the second leaf is formed very early and this stele joins the primary axial bundle of the young sporophyte. A similar leaf trace is formed in each succeeding leaf up to about the seventh. At this stage, except for the steles of the secondary roots, the vascular system is built up of united leaf traces and there is no true cauline stele, although one might refer to the solid central cylinder of the axis formed by the fusion of the early leaf traces as the "stele" of the "stem." The primary bundle is never a true "protostele," since the xylems belonging to the component

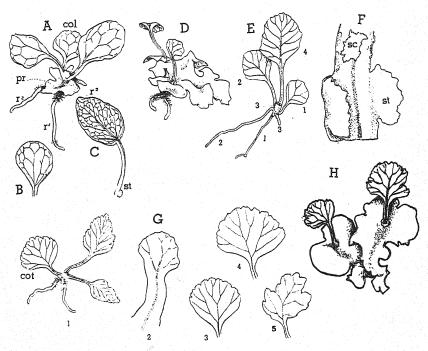


Fig. 188.—Young sporophytes of Marattiaceae. A, B, C, Kaulfussia; D, E, F, Danaea; G, H, Angiopteris; cot, cotyledon.

leaf traces can be recognized and the compound nature of the older stele is unmistakable.

About the time the seventh leaf is formed in *Danaea* there is developed a single axial strand, which is not of foliar origin but can be traced directly to the apical meristem of the axis and is therefore a true cauline structure. This is the commissural strand. The leaf traces formed subsequent to the development of the commissural strand are double. In the older sporophyte the vascular skeleton is an open, wide-meshed cylinder or dictyostele, within which is the commissural strand or strands.

The early leaves retain the simple lamina but sooner or later develop in most cases a ternate form resembling the cotyledon of *Botrychium* or the first foliage leaf of *Helminthostachys*. By degrees the pinnate form of the adult frond is attained.

CLASSIFICATION

The Marattiaceae have been divided into the subfamilies Kaulfussieae, Danaeieae, Marattieae, and Angiopterideae. Of these the subfamily Kaulfussieae, with the single genus Kaulfussia (Christensenia), is, on the whole,

the simplest type and most like the Ophioglossaceae. It differs so much from the other Marattiales that it might well be recognized as a distinct family, Kaulfussiaceae.

The other genera are sufficiently alike in their general structure to indicate a fairly close relationship and might be retained in the single family Marattiaceae. Moreover, although the Angiopterideae have completely distinct sporangia, they are connected by intermediate forms with the Danaeieae, which, omitting Kaulfussia, are probably the most primitive of the living Marattiaceae. Angiopteris is the most specialized and apparently has diverged most widely from the ancestral type. The other genera, Macroglossum and Archangiopteris, in the leaves and the structure of the sporangium, are intermediate between Angiopteris and Danaea. They have simply pinnate leaves, and the sori are much elongated like the synangia of Danaea. In Macroglossum the sporangia are closely set and the sorus is sunk in a groove, so that the sorus superficially looks very much like the elongated synangium of Danaea. The individual sporangium is simpler than that of Angiopteris and the annulus is imperfectly developed.

The Marattieae include about thirty-five species of Marattia, found throughout the tropics of both hemispheres. One species, M. salicifolia, reaches South Africa. A second genus, Protomarattia, recently found in Tonking, has a prostrate rhizome and simply pinnate leaves like Archangiopteris. The synangium is of the Marattia-type but is more elongated and suggests an approach to Danaea.

FOSSIL MARATTIALES

Unlike the Ophioglossales there are numerous fossils the leaves of which are similar to those of most of the living Marattiaceae and which bear sporangia (or synangia) which in position and structure indicate a real relation to the Marattiaceae. In some of them the sporangia were free, like those of the Angiopterideae; in others they were more or less completely fused to form synangia. These fossil Marattiales are especially abundant in the later Carboniferous.

ORDER ISOETALES

The genus *Isoetes*, the sole representative of the family Isoetaceae, differs so much from the other pteridophytes that there has been some difference of opinion as to its nearest relatives. It is most commonly associated with *Selaginella*, with which it agrees in being heterosporous and in showing some marked resemblances in the spores and gametophyte. There are, however, some very good reasons for the conclusion that *Isoetes* is more nearly related to the eusporangiate Filicineae. Whether the relationships are with the Lycopodineae or with the Filicineae, it is evident that

Isoetes is sufficiently distinct to warrant the establishment of an order, Isoetales.

Isoetes is practically cosmopolitan; but the majority of the sixty or more described species belong to the Northern Hemisphere. About twenty species are found in the United States. They are mostly submersed aquatics or amphibious, but some of them are terrestrial.

The short, thick stem is completely covered by the broad overlapping bases of the narrow, rush-like leaves, and the plant recalls such simple monocotyledons as *Lilaea* or *Triglochin*. They are perennials, and the older

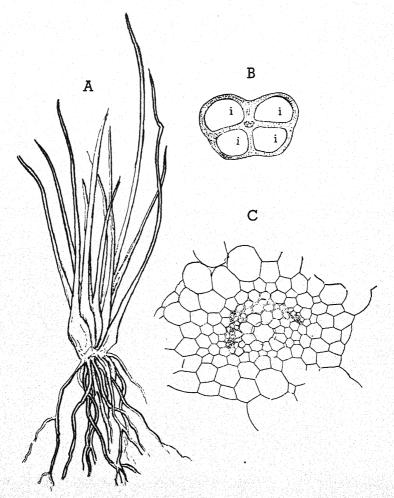


Fig. 189.—A, Isoetes eclinosporia var. Braunii; B, section of leaf; i, lacunae; C, vascular bundle of leaf.

stems show two or three broad lobes separated by deep furrows on the lower surface of the stem. The roots, which are dichotomously branched, like those of the Lycopodineae, and formed in acropetal succession, are borne within the furrows. The stem shows a secondary growth in thickness.

All of the leaves are fertile except those produced at the end of the growing season. Each leaf has a very large oval sporangium borne on the adaxial side of the expanded base of the leaf. The sporangium lies in a depression ("fovea") whose margins form a membrane ("velum") covering more or less completely the free surface of the sporangium. The velum may perhaps be compared with the indusium of the ferns. Above the sporangium is a conspicuous ligula much like that found in Selaginella.

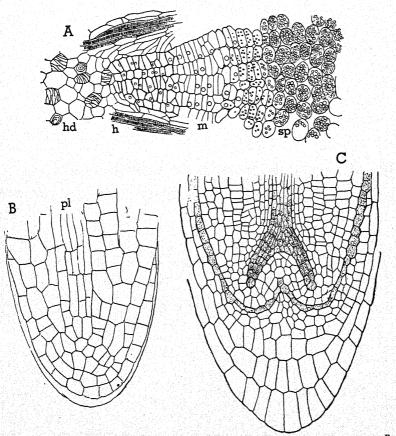


Fig. 190.—A, transverse section of stem of Isoetes lacustris; m, meristematic zone; B, section of second root of I. eclinosporia; pl, plerome; C, root of I. lacustris showing dichotomy (A, after Potonié; C, after Bruchmann).

The first-formed leaves of each growth cycle produce the megasporangia and the later ones the microsporangia. At the end of the season the young leaves are imperfect, the sporangia being aborted or entirely absent. The circle of imperfect leaves marks the limits of the successive growth periods.

The stem.—In the stem of the young sporophyte the fibrovascular system is made up entirely of the union of leaf traces and root bundles, in this respect closely resembling the condition in the Ophioglossaceae and the Marattiaceae. This condition holds also for the older sporophyte; but Scott and Hill, in a study of a terrestrial species, *I. hystrix*, state that a cauline stele is developed.

In section the stem shows a central region composed of short tracheids mingled with similarly shaped parenchyma. Surrounding this xylem is a cylinder of prismatic cells sometimes regarded as phloem. Outside the phloem there is a region of actively dividing tissue, the cambium, from which new cells are added within to the phloem; but sometimes short tracheids are also formed. This secondary thickening of the stem is evidently very different from that in *Botrychium*, where the cambium develops

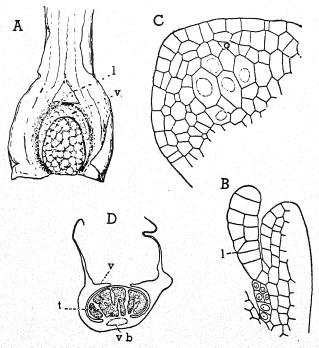


Fig. 191.—A, leaf base of *Isoetes echinospora* with megasporangium; l, ligule; v, velum; b, section of young sporophyll; l, ligule; c, section of young megasporangium; d, cross section of microsporangium; v, velum; t, trabeculae; vb, vascular bundle (B-D), after Wilson-Smith).

xylem within and phloem without—like the secondary thickening in the conifers and dicotyledons. The condition in *Isoetes* has been compared with that in some of the arborescent monocotyledons like *Yucca* and *Dracaena*.

The leaf.—A cross section of the leaf in I. Braunii shows four large air spaces, or lacunae, separated from each other and from the epidermis of the leaf by several layers of cells. There is a simple axial collateral vascular bundle. The lacunae are divided by a series of transverse diaphragms. The primary leaf of the young sporophyte has two lacunae, and a cross section of it is very much like that of the petiole of the cotyledon of Ophioglossum moluccanum, which also has two lacunae and a median collateral bundle.

In the terrestrial species and those which are only partially submersed there are numerous stomata, which may be entirely absent in the submersed leaves.

The root.—The roots originate near the leaf base. There is no apical cell and the arrangement of the primary tissues is much like that in Lycopodium and also recalls the roots of the angiosperms. Farmer states that in I. lacustris the central cylinder (plerome) has a single initial cell, above which are two layers of meristem cells, the inner one belonging to the inner cortex, the outer giving rise to the outer cortex, the epidermis, and the root cap. The branching of the root is dichotomous, recalling the Lycopodineae; but the roots of Ophioglossum may also show dichotomy, and the vascular bundle of the root in Isoetes is monarch as in Euophioglossum.

The sporangia.—The development of the sporangium has been investigated very thoroughly by Bower and by Wilson-Smith. The sporangium develops from a small group of superficial cells on the inner face of the leaf base. The young sporangium forms an oblong cushion, and very early in its development the growth of the adjacent tissue forms the fovea, which with the indusium, or velum, formed from its margin, encloses the young sporangium. The relation of the sporangium to the indusium is somewhat like that of the nucellus of an ovule to the integument.

In the young sporangium, by a series of periclinal divisions, a central mass of potentially sporogenous tissue is separated from several layers of parietal cells forming the wall of the sporangium. There is no difference in the appearance of the mega- and microsporangia until the late stage in the development of the sporogenous tissue. This at first is composed of uniform cells but later becomes differentiated into sterile and fertile areas. There are definite areas of sterile cells partly enclosing masses of sporogenous tissue. Sections of the central portion of the sporangium show the sterile tissue forming incomplete septa or "trabeculae" between the masses of spores. The process is very much like the development of the synangium

in some of the Marattiaceae, especially Danaea. There is also a certain resemblance to the young sporangiophore of Ophioglossum.

The cells of the trabeculae, which are in contact with the masses of sporogenous cells, and the innermost cells of the sporangium wall function as a tapetum.

In the microsporangium all the sporogenous cells develop into spore mother cells. The final divisions are successive and the resulting spores are "bilateral" instead of tetrahedral. The number of microspores is very large, sometimes as many as 300,000 or more. Unlike Selaginella there is no marked difference in size between the two sorts of sporangia in Isoetes, and instead of the (usually) four megaspores found in Selaginella there may be in Isoetes as many as three hundred.

Only a relatively small number of the sporogenous cells in the megasporangium develop into spore mother cells. Even before the differentiation of the trabeculae, some of the sporogenous cells grow more rapidly than their neighbors and are recognizable as the future spore mother cells. These finally become very large and undergo the characteristic division into the tetrad of megaspores.

The development of the megaspore has been investigated by Fitting. There is a certain likeness to the early megaspore development in Selaginella, but there is a radical difference. In Selaginella the young megaspore is nourished directly from the outer tissues of the sporangium with which it is in close contact, and the germination of the spore and the early stages of the enclosed gametophyte are completed before the spores are discharged from the sporangium; in short the gametophyte is parasitic upon sporophytic tissues. In Isoetes the ripe megaspore has but a single nucleus and germination does not begin until the spores are discharged from the sporangium. The ripe spore is filled with food materials upon which the young gametophyte depends for its growth.

The mother cell of the megaspore tetrad has a large nucleus and abundant granular contents. The granules include a mass of starch grains which divide into four groups before the nucleus divides. At this stage the mother cell recalls the corresponding stage in *Anthoceros*. After the second division of the nucleus each of the four daughter nuclei is in close contact with one of the starch groups. This is followed by the simultaneous formation of walls between the nuclei, resulting in the four tetrahedral spores.

The protoplast of each young spore secretes the special membrane from which the outermost coat, the "epispore," is developed. This is marked by characteristic spinules or tubercles. Within the epispore are later developed the three other membranes, viz., exospore, mesospore, and endospore. At one stage the protoplast becomes partially free from the mesospore, but this is much less marked than in Selaginella.

The gametophyte.—The ripe spores are set free by the decay of the sporangium wall. The microspores are very small bean-shaped cells. The first division of the nucleus is followed by a wall cutting off a small vegetative, or prothallial, cell from a much larger one. In the latter a series of divisions result in a group of four central cells surrounded by four peripheral ones, the whole structure probably representing a single antheridium. The male gametophyte of *Isoetes* is the most reduced form known in the pteridophytes. Each of the four central cells becomes at once a spermatocyte, in which is formed a spirally coiled, multiciliate spermatozoid, like that of the ferns, instead of the biciliate spermatozoids of the Lycopodineae.

The large tetrehedral megaspore is filled with dense granular contents and a single very large nucleus. In I. Braunii (= I. echinospora var. Braunii) the nucleus is at the base of the spore, where it undergoes the first divisions. The secondary nuclei move to the apex of the spore, where they divide repeatedly before any cell walls are developed. After about fifty free nuclei have been formed, cell division begins in much the same way as in Selaginella, cell walls being formed simultaneously between the free nuclei, resulting in a layer of cellular tissue at the apex of the spore. Cell division continues along the periphery of the spore cavity, and for a

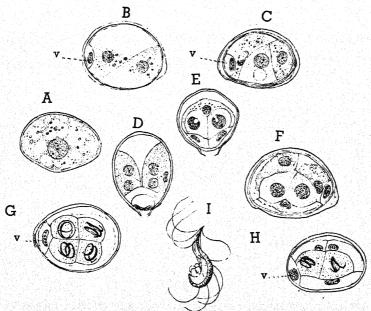


Fig. 192.—A-F, development of male gametophyte in I. echinospora; C, H, two views of mature gametophyte; v, prothallial cell; I, spermatozoid of I. malinverniana (I, after Belajeff).

time the central portion remains undivided. Finally the whole spore is filled with cellular tissue. The development of the gametophytic tissue is much like that of the endosperm of the seed plants.

The first archegonium is formed early in the development of the game-tophyte. In *I. Braunii* two secondary ones are formed later. If none of these are fertilized there may be several additional ones. The gametophyte has no chlorophyll and is dependent upon the food contained in the spore.

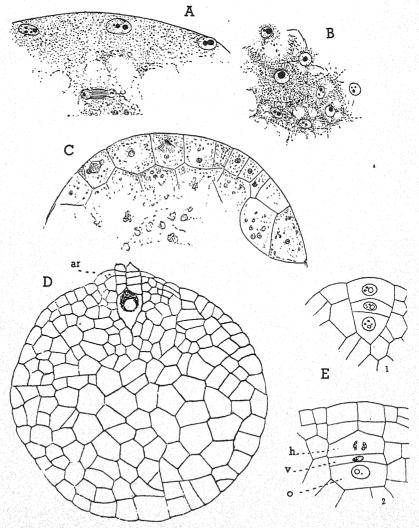


Fig. 193.—A-C, early stages of development of the female gametophyte of I. echinospora; D, older gametophyte with archegonium; E, young archegonia.

The embryo.—In I. Braunii the basal wall in the embryo is transverse but may be more or less oblique. There may sometimes be a regular quadrant division, but generally the early divisions are somewhat irregular. Of the two primary cells the epibasal gives rise to the cotyledon and root and later to the stem apex, while from the hypobasal cell the foot is developed. The arrangement of the organs of the young sporophyte is not unlike that of the eusporangiate ferns. The embryo of Botrychium virginianum perhaps most nearly resembles that of Isoetes, but there are resemblances to the embryo of the Marattiaceae also. There is, however, in Isoetes no definite apical cell in either root or cotyledon.

In its earlier stages the embryo is an oval mass of similar cells. It next becomes more elongated in the plane of the basal wall and the epibasal portion is differentiated into the cotyledon and root, which grow in opposite directions. At the base of the cotyledon is a large cell which becomes the

ligule.

Soon after the ligule is first recognizable a semicircular ridge is formed at the base of the root and, growing rapidly, encloses the base of the leaf

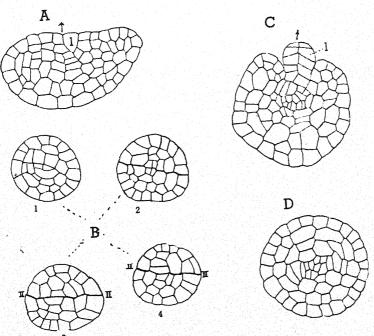
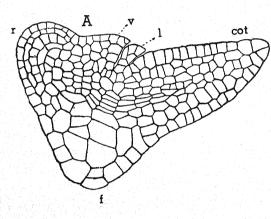


Fig. 194.—A, median longitudinal section of embryo of Isoetes echinospora; I, ligule; B, four horizontal sections of a young embryo of the same; C, D, two transverse sections of an older embryo, showing axial vascular bundle and ligule.

together with the ligule. At the bottom of the cleft between the sheath and the leaf base an inconspicuous group of cells marks the beginning of the future stem apex, of which there is no indication in the younger embryo and which shows no definite apical cell.

The axes of the cotyledon and primary root may coincide, but this is not always the case. The young vascular bundles of the two organs are continuous, as they are in the Ophioglossaceae and the Marattiaceae. The arrangement of the tissues in the young primary root have their nearest counterpart in some of the simpler monocotyledons, e.g., Naias flexilis.

The foot in the younger embryo is not clearly differentiated, but as the



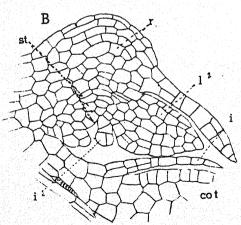


Fig. 195.—A, median longitudinal section of older embryo of *I. echinospora; cot*, cotyledon; *f*, foot; *r*, root; *v*, velum; *l*, ligule; *B*, apical region of a young sporophyte with the second leaf, *l*², already formed; *st*, stem apex.

young sporophyte develops it becomes greatly enlarged and gradually nearly fills the spore cavity so that almost nothing is left of the prothallial tissue.

RELATIONSHIPS OF THE EUSPORANGIATAE

The Eusporangiatae, as they now exist, are but remnants of what in earlier geological time was presumably a very much larger and more varied assemblage. While the three genera of the Ophioglossales differ from each other in a good many details, their essential structures are sufficiently alike to indicate that they are really related, and the same is true of the several genera of the Marattiales, except possibly Kaulfussia.

Of the living ferns there is good reason to believe that the Ophioglossaceae are the most primitive. Unfortunately, perhaps owing to their delicate tissues, practically nothing is known of their past history. It is possible that the Devonian and Early Carboniferous

Coenopteridales were remotely related to the Ophioglossales.

The recent discoveries of the exceedingly simple mid-Devonian Psilophytales may throw some light upon the origin of the Ophioglossum-type. The resemblances in the young sporophytes of Ophioglossum and Anthoceros are also suggestive of a remote relationship. Like the sporophyte of the simplest known vascular plants, the Rhyniaceae, the young sporophyte of Ophioglossum moluccanum at first is rootless, consisting simply of the cotyledon and the foot. This condition is comparable to the sporophyte of Anthoceros.

The dichotomously branched plant body of the Rhyniaceae, the telome without definite leaves and roots, may show a differentiation into fertile sporangiophores and sterile phylloids. In *Euophioglossum* the primordium of the fertile frond divides into two equal parts, one forming the sporangiophore, the other the sterile leaf lamina, which might be compared to the

two branches of a telome in the Rhyniaceae.

We might perhaps imagine two types of "pro-ferns" derived from Anthoceros-like ancestors: one through the Psilophytales resulting in a broad dichotomously branched frond, bearing marginal sporangia, e.g., Cladoxylon; the other giving rise more directly to the sporangiophore of the Ophioglossum-type. In Anthoceros there may be a quite definite alternation of fertile and sterile tissue, suggesting a segregation of the sporagenous tissue into distinct areas. There might thus result a series of simple sunken sporangia with marginal dehiscence, as in Ophioglossum, rather than the single terminal sporangium of the Rhynia type.

The derivation of the much-branched sporangiophore of Botrychium, with its free sporangia, from the solid spike and sunken sporangia of Ophioglossum is quite comprehensible. A relation between the sporangiophore of Ophioglossum and the synangium of the Marattiaceae situated on

the abaxial surface of the leaves is not so readily explained.

While the similarity in the development of the synangium in Danaea and the sporangiophore of Ophioglossum is notable, the conclusion that the two organs are really homologous might well be questioned. It is conceivable, however, that from some Ophioglossum-like form, with several small marginal sporangiophores like those of O. palmatum, there might result a condition not unlike that in Danaea simplicifolia by the shifting of these sporangiophores (or synangia) to the lower surface of the leaf.

While the more specialized Marattiaceae, like Angiopteris and Marattia, seem to have little in common with the Ophioglossaceae, a study of the development of the more primitive genera Danaea and Kauljussia shows such significant similarities in structure between them and the Ophio-

glossales as to indicate a degree of relationship warranting the inclusion of the two orders in the Eusporangiatae. Of the Ophioglossaceae, *Helminthostachys* is most like the Marattiales, while *Kaulfussia* of the latter order approaches nearest to the Ophioglossaceae.

Unlike the Ophioglossaceae the Marattiales are represented by many fossil types, especially in the later Palaeozoic. Some of these, like Psaronius, were tree ferns with lofty trunks and ample fronds. Many fossil leaves having the "pecopterid" venation, like that of most of the living Marattiales, have been tentatively assigned to this order and some of these, with the sporangia or synangia attached, are generally admitted to belong to the order. These are most abundant in the Upper Carboniferous. Of these fossil types the following genera may be cited: Ptychocarpus, Asterotheca, Senftenbergia, Danaeites. The Mesozoic genera, Danaeopsis and Marattiopsis, are evidently related to the modern genera.

Bower, in discussing the fossil Marattiales, states that in all of them the leaf segments are narrower than in the living types and suggests that they may have been derived from forms having sporangiophores like those of the Ophioglossaceae, where the sporangia are marginal. With the expansion of the leaf surface the marginal sporangia (or synangia) might be gradually transferred to the abaxial surface. Of the living genera, Danaea is the only one in which the fertile leaf segments are notably contracted, closely resembling the condition in the fossil types, especially Danaeites.

While in form and the coiled condition of the young leaves the Maratitaceae are much more like the typical ferns than like the Ophioglossaceae, nevertheless in the anatomical structure they have more in common with the Ophioglossales. In both orders pinnate and reticulate venation are found. Whether this is a case of parallel development or indicates a possible connection of the two orders at different points is an open question.

The early development of the sporophyte in the two orders has much in common and suggests that the ancestral "pro-fern" consisted simply of a sporangiophore (or leaf) and a foot. The embryo of *Ophioglossum moluccanum* most nearly approaches this condition. The development of a root is secondary, and in the Marattiaceae the very young embryo consists only of the cotyledonary region and the foot.

In both orders the young sporophyte is bipolar, being composed mainly of the cotyledon and the root, traversed by a common vascular bundle. In *Ophioglossum moluccanum* there is no stem in the young sporophyte, and in the Marattiaceae the stem apex is little developed and no stelar tissue is developed from it. In *Ophioglossum* the whole vascular system of the axis is built up exclusively of leaf traces, and this is true of the early stages in the Marattiaceae. In the latter, however, there are later developed within

the dictyostele, formed by the leaf traces, a number of independent cauline commisural bundles.

The two orders agree in the absence of mechanical tissues in the stem, these tissues being a common feature of the Leptosporangiatae. In the massive leaves of the Marattiaceae both collenchyma and sclerenchyma may be present. These are mostly absent from all parts of the Ophioglossaceae. The collateral vascular bundles of the Ophioglossaceae probably represent the more primitive type from which the concentric bundles of most of the Marattiaceae have been derived. Concentric bundles occur in the petioles of Botrychium, and on the other hand collateral bundles are found in the voung sporophyte of Danaea.

The subterranean gametophyte of the Ophioglossaceae, quite destitute of chlorophyll, differs greatly from the large green prothallium of the Marattiaceae. The latter, however, shows the presence of an endophytic fungus like that of the Ophioglossaceae but much less developed, and perhaps indicating a limited symbiotic association. While it seems probable that the green gametophyte of the Marattiaceae is a more primitive condition than the saprophytic gametophyte of the Ophioglossaceae, the occurrence of subterranean gametophytes in the two primitive orders, Psilotales and Lycopodiales, indicates that this is not a recent adaptation. It may be recalled that a somewhat similar relation exists in the Anthocerotes, although the endophyte is a blue-green alga and not a fungus.

RELATIONSHIPS OF ISOETES

While the systematic position of *Isoetes* is very uncertain, there is evidence of a real, if remote, relationship between it and the Eusporangiatae. The general morphology and anatomy of its sporophyte is much more like that of the Ophioglossaceae and Marattiaceae than that of Lycopodiales, although there are certain marked resemblances with the latter, notably the ligulate leaves, which recall *Sclaginella* and the early stages of the gametophyte. The vascular bundles are collateral, like those of *Ophioglossum*, a type found also in the spermatophytes.

The sporangium, although in position like that of Lycopodium, is structurally much more like Danaea and might be called an imperfect synangium rather than a simple sporangium. In Danaea the synangium is in a depression which might be compared to the fovea of Isoetes. Professor Bower compares the sporangium of Isoetes with that of Lepidodendron; but the derivation of such a delicate aquatic plant with only sporogenous leaves, with an arborescent form having definite strobili, requires much more evidence than is at present available. The aquatic habit of Isoetes is also indicative of relationship with the ferns, as all of the heterosporous

ferns are aquatic, while Selaginella is terrestrial and some species decidedly xerophytic.

The early development of the female gametophyte is certainly much as in *Selaginella*; but, as in the heterosporous ferns, e.g., Marsileaceae, germination does not take place until the spores are discharged from the sporangium. The similarity of the archegonium and embryo of *Isoetes* to those of the Eusporangiatae and especially the multiciliate spermatozoids, are strong evidence of filicinean relationship.

In a recent paper (*Jour. Wash. Acad. Sci.*, June 1939), Roland W. Brown treats at length the records of fossil Isoetales. He describes two Cretaceous species of *Isoetetes*, which he concludes are related to *Isoetetes*.

While the similarity in structure of the micro- and megasporangia indicates a less advanced condition than in the other heterosporous genera, the male gametophyte is more reduced than in any other pteridophyte. The microspore, with its enclosed gametophyte, producing only four male cells, may be compared with the pollen spores of the lower seed plants. In short, while there are important differences which are not easily explained, it seems by no means impossible that the Isoetaceae may have been derived from some homosporous eusporangiate type.

The marked similarity in habit and the resemblances in the embryo and anatomy of the older sporophyte between *Isoetes* and some of the lower aquatic monocotyledons have suggested a possible development of some of these from *Isoetes*-like ancestors; but the differences between the simplest angiosperm flower and the sporophylls of *Isoetes* are so great that much more evidence than is now at hand will be necessary to support this hypothesis.

CONCLUSION

The Eusporangiatae, as they now exist, may be regarded as remnants of widely divergent branches of a common primitive Palaeozoic stock which have been largely supplanted by more specialized modern types. Of these the leptosporangiate ferns are especially noteworthy. Several lines of seed-bearing plants are to be traced to the same source. One line of these, the pteridosperms, is entirely extinct. Others, like the cycads and conifers, have survived to the present time but have been largely replaced by the angiosperms, the dominant types of the modern floras. The origin of the angiosperms is very obscure but it seems probable that they were derived independently from the eusporangiate stock through some heterosporous forms, possibly resembling *Isoetes*, and not from the gymnosperms.

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CHAPTER XV

LEPTOSPORANGIATAE: EUFILICINEAE, OSMUNDACEAE, GLEICHENIACEAE

The great majority of the living ferns belong to the Leptosporangiatae. The number of recognized species exceeds six thousand, while the total of the Eusporangiatae scarcely reaches three hundred.

The typical leptosporangiate ferns have the sporangium developed from a single epidermal cell, but there are some exceptions in the more primitive forms, like Osmunda, where there is some approach to the more massive eusporangiate type; so that the distinction between the eusporangiates and the leptosporangiates is not absolute. The Leptosporangiatea, like the Bryales among the mosses, are evidently relatively modern, specialized forms which have to a great extent superseded the less adaptable eusporangiates.

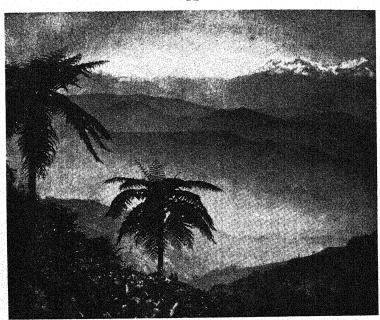
While the Eusporangiatae are few both in species and usually in numbers of individuals, and are quite absent from many regions, the Leptosporangiatae are cosmopolitan and often form a prominent feature of the floras of many parts of the world, especially in the mountain rain-forests of the tropics and in oceanic islands like New Zealand and Hawaii. Occasionally, even in the northern countries, the common bracken may take possession of large areas almost to the exclusion of other vegetation. The not uncommon belief that the living ferns, like the club mosses and horsetails, are merely remnants of an ancient, more luxuriant vegetation is scarcely borne out by the facts; and anyone who has seen the extraordinary variety and luxuriance of the fern floras of such mountain regions as Jamaica or Hawaii, or the lowland forests of New Zealand realizes how unfounded is this belief. It is doubtful if any fossil ferns equaled in size some of the living tree ferns.

While the majority of the leptosporangiates require abundant moisture for their normal development and reach their maximum in the rain-forests, a very considerable number are "xerophytes" and are capable of enduring prolonged periods of drought. Thus in coastal California some of the commonest species, e.g., Polypodium californicum, Adiantum emarginatum, and others, dry up completely during the long rainless summer. Many epiphytic species in the tropics also remain dormant during dry periods. Aquatics are not numerous, but the water-ferns, "Hydropterides"—e.g., Marsilea, Azolla, Salvinia—are true aquatics and the striking fern, Acrostechum aureum, inhabits the mangrove swamps in all tropical regions.

In size they range from tiny filmy ferns (Hymenophyllaceae) with thread-like rhizomes bearing leaves a centimeter or less in length to giant tree ferns with massive trunks ten or fifteen meters high and with a crown of leaves three meters or more in length. In spite of the great range of size the general structure is much alike but shows somewhat the same differences that were noted in the Marattiaceae, to which the Leptosporangiatae are most nearly related.

The stem.—The stem may be a prostrate dorsi-ventral rhizome with scattered leaves; but more commonly it is a short, upright stock with closely set, spirally placed leaves. Where the stem is a prostrate rhizome, as in the common bracken, it may branch freely, the branching being





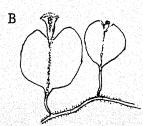


Fig. 196.—A, a tree fern, Alsophila, sp.; B, a filmy fern, Trichomanes Motleyi, × 5.

monopodial. In the ostrich fern, *Matteuccia*, the stout caudex may develop adventive slender stolons very different from the primary stem.

In most of the common ferns the vascular system is a dictyostele like that in the Marattiaceae. Whether or not this dictyostele is composed exclusively of leaf traces remains to be seen; but it is quite likely that this

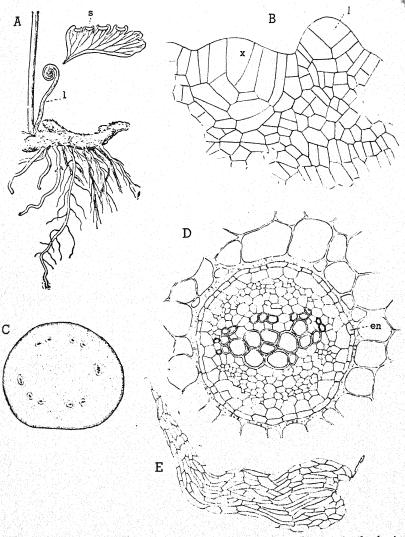


Fig. 197.—A, rhizome of Adiantum pedatum; I, young leaf, above a pinnule showing marginal sori, s; B, stem apex of Adiantum emarginatum; x, apical cell; I, young leaf; C, section of rhizome of Polypodium falcatum; D, vascular bundle of the same; en, endodermis; E, scale from stipe of Cystopteris fragilis.

is the case, although it is generally held that the dictyostele in the Leptosporangiatae is a truly cauline structure. Cauline bundles are present in *Pteridium aquilinum*, but these are exceptional. There may be a single axial stele in the stem, but more often there is a dictyostele probably formed by the union of leaf traces. The bundles are concentric, with a very evident endodermis; and the structure and arrangement of the bundles is very like that in most of the Marattiaceae. Bower considers the dorsiventral rhizome with a single axial stele (protostele) and remote dorsal leaves as the more primitive condition. This would be in harmony with the theory that the primitive fern was monophyllous.

The leaf.—The leaves are in most cases compound and may reach a great size, in general resemble in form the Marattiaceae but are generally less fleshy in texture; occasionally they are membranaceous and may, in the Hymenophyllaceae, consist of a single cell layer. They may, however, be firm and leathery. Like the Marattiaceae the young leaves are closely coiled (cincinnate) in the bud. The surface may be quite smooth, or there may be various epidermal appendages—hairs and scales—especially developed in the younger parts.

The leaves are most commonly pinnately compound; but simple leaves are found in a good many genera, e.g., Scolopendrium, Camptosorus, Vittaria, Asplenium Nidus; and dichotomous division is characteristic of a number of genera, e.g., Gleichenia, Dipteris Matonia, and Schizaea.

The vascular bundles of both stem and petioles (except in the stem of Osmundaceae) are concentric, thus resembling the Marattiaceae rather than the Ophioglossaceae. In the smaller veins of the leaf, however, the vascular bundles are more or less definitely collateral. In the older cortical tissue of leaf and stem there is commonly a marked development of dark-colored sclerenchyma.

The structure of the sporangium in all of the Leptosporangiatae is much the same. In the great majority it can be traced back to a single epidermal cell on the abaxial surface of the leaf. The early growth is from a tetrahedral apical cell. The growth of this is checked by the formation of a periclinal wall, which results in a central tetrahedral cell surrounded by a layer of peripheral cells. From the central cell a series of segments are formed, which give rise to the tapetum, the central cells becoming the archesporium.

POLYPODIACEAE

The stem.—The stem apex of the Polypodiaceae, which include most of the Leptosporangiatae, is a slightly conical prominence having a large tetrahedral apical cell with very regular segmentation at first. The primary tissues of the axis are soon clearly marked. From the inner cells

the pith and vascular bundles arise, from the outer ones the cortex and

epidermis.

In the outer cortical region there is generally the development of dark-colored sclerenchyma, which sometimes may form the greater part of the ground tissue. In section these stem bundles are elliptical or elongated in outline and have a very definite endodermis or bundle sheath. In the elliptical bundle the protoxylem forms two groups of narrow spiral or reticulate tracheids at the foci of the bundle section. From these points the development of the large metaxylem elements proceeds toward the center of the bundle and finally forms a complete band between the two

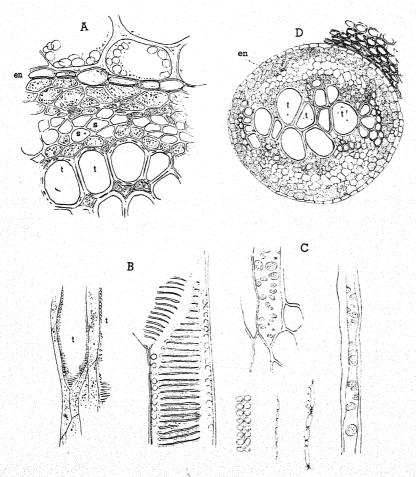


Fig. 198.—A, portion of a vascular bundle from the rhizome of Woodwardia Chamissoi; B, tracheids of the same; C, sieve tubes; D, vascular bundle of root of Woodwardia.

protoxylems. The metaxylem tracheids are larger, with transversely elongated bordered pits—the "scalariform" tracheids characteristic of the fern bundles. In the xylem there are also elongated parenchyma cells. Completely enclosing the xylem is a zone of phloem made up of mingled phloem, parenchyma, and conspicuous sieve tubes. The latter have numerous sieve plates both on the lateral walls and at the ends of the cells. Outside the phloem is the pericycle composed of one or two cell layers, and surrounding the bundle is the endodermis. Strasburger states that the pericycle and endodermis belong to the cortex and are not part of the vascular bundle.

The leaf.—Owing to the slow formation of segments in the apical cell of the stem, it is uncertain whether or not each of the segments gives rise to a leaf; but this is not unlikely. The young leaf is a blunt cone with a large apical cell, which, usually at least, forms two rows of segments. As it grows the young leaf assumes the form of a flattened cone with broad base, more convex on its outer side, where growth is more rapid and the young leaf begins to show the characteristic coiled form. The lower portion grows more rapidly and forms the petiole, which develops much faster than the lamina, which remains small until the close of the season before

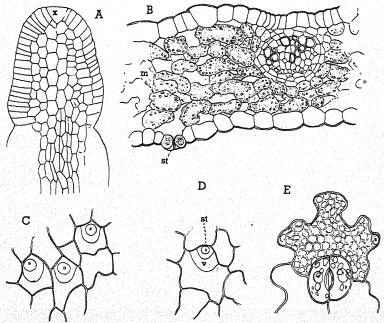


Fig. 199.—A, apex of young leaf of Onoclea Struthiopteris; B, section of leaf lamina of Polypodium falcatum; C-E, development of the stoma in Adiantum emarginatum; v, accessory cell.

it unfolds. As in the Ophioglossaceae the development is very slow and in colder climates may take three or four years. The last stage of growth consists mainly in expansion of the lamina with comparatively little cell division.

In species with pinnate leaves the development of the pinnae begins soon after the separation of the leaf into petiole and lamina can be seen. Each segment of the apical cell forms a pinna. Their formation is strictly monopodial and begins by an increase in growth in the outer cells of the young segment, which thus forms a marginal lobe. The growth of the young pinna is not from a single apical cell. As each pinna corresponds to a segment of the apical cell of the leaf, it follows that they alternate with each other on opposite sides of the rachis. Where the leaves are bipinnate it is probable that the primary pinnae develop a definite apical cell.

The midrib of each lobe of the pinna bears the same relation to it that the rachis of the frond does to the pinna itself. The secondary veins arise in acropetal succession, and at first consist of a strand of procambium extending from the midrib to the margin. Where dichotomy of the final veins occurs, it is connected with a dichotomy of the marginal group of meristematic cells. Except for the smallest veins which have collateral bundles, the bundles of the leaf are concentric like those of the stem, and the petiole (stipe) shows much the same structure as the stem.

The structure of the lamina is very much like that of the Marattiaceae. Stomata are most commonly found only on the abaxial surface of the leaf, but there are many exceptions. Where stomata are absent from the upper epidermis there may be developed a palisade hypodermal tissue; but it is less marked—at least in most ferns—than is the case in some of the Marattiaceae. The bulk of the mesophyll is composed of very irregular cells with large intercellular spaces. The formation of a stoma in the Polypodiaceae is preceded by the formation of a curved wall cutting off a small cell from an epidermal cell. A similar wall within this cell forms the stoma mother cell. The stoma itself is of the same type as that in most other vascular plants.

Most of the Leptosporangiatae develop various epidermal appendages—hairs or scales—especially abundant on the younger parts and evidently protective in function. The hairs (and sometimes the scales) bear glands which secrete mucilaginous matter, or less often a resinous secretion. The large chaffy scales (paleae) found on the leaf bases of so many ferns are especially characteristic.

The root.—In most ferns the roots are formed in large numbers. According to Van Tieghem they always arise from an endodermal cell of a vascular bundle of the stem. This divides into an inner and outer cell, the former connecting the young root with the xylem of the stem bundle.

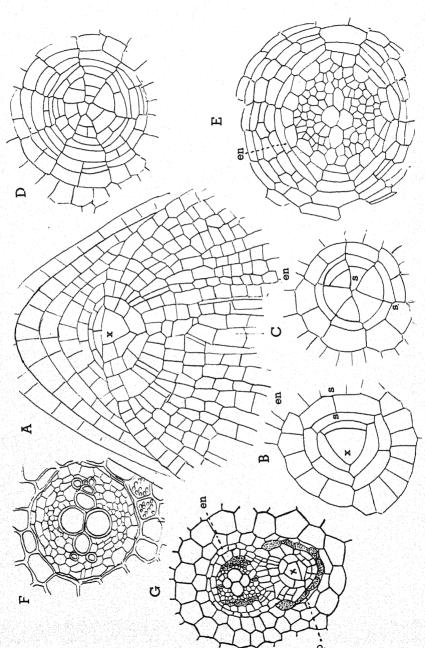


FIG. 200.—4, longitudinal section; B-E, series of cross sections of root of Adiantum emarginatum; F, vascular bundle of root of Adiantum pedatum; G, formation of a lateral root in Pteris cretica; x, apical cell of rootlet; p. "digestive pouch" (G, after Van Tieghem).

At an early period a very definite tetrahedral apical cell, with extremely regular segmentation, is developed. Segments are cut off in regular succession from all four faces of the apical cell. Those from the outer free face contribute to the root cap; the lateral segments to the other tissues of the root. The first-formed cap segments are continuous with the epidermis and remain but one cell thick; in the later cap segments there is normally a doubling of the cells by periclinals, so that each layer of the older root cap is normally double.

The first division in each lateral segment is a sextant wall, the two cells being somewhat unequal in size. Each sextant is divided into an inner and outer cell which establishes the "plerome" or primary stele from the cortex (periblem). A further division in the latter separates the primary epidermis. There is very little displacement of the cells for a long time. and cross sections in the younger part of the root still show the limits of the sextant walls with periclinal walls arranged with great regularity. In the plerome, cell division is rapid, transforming it into a cylinder of elongated procambium cells. The axial procambium cells are larger and mark the beginning of the tracheary tissue of the older root. The young stele is bounded externally by the endodermis, within which lies the pericycle consisting of one or two layers of cells. The primary tracheids (protoxylem) are formed at the foci of the slightly elliptical region. These tracheids are very narrow, with fine spiral markings. The large metaxylem elements between the two protoxylems are much larger, with scalariform markings like those of the stem bundles. The cells of the pericycle are little changed: but there are two phloem masses in which are developed characteristic sieve tubes. The stele of the root is therefore "diarch," which is the case in most of the Leptosporangiatae.

The secondary roots arise in regular succession in two series corresponding to the position of the protoxylems of the diarch bundle. The secondary roots may also branch further and an extensive root system is thus developed. In a very few cases no true roots are formed. Thus Salvinia and some species of Trichomanes are rootless, but either modified leaves (in Salvinia) or rhizomes function as roots.

The sporangium.—The development of the sporangium in all the Leptosporangiatae is essentially much the same. In the Polypodiaceae the sporangia are usually formed in definite groups, or sori, upon the abaxial surface of the frond. In most genera, as in most of the Marattiaceae, there is no marked difference in size or form between the sterile fronds and the sporophylls. Occasionally, e.g., in *Onoclea*, the sporophylls are much smaller and the lamina are contracted.

In *Polypodium*, which will serve for illustration, the sporangia form a circular naked sorus. In most other genera the sorus is covered by a

protective membrane, or indusium, which is an important factor in classification.

The sporangia are borne upon a slight elevation, the placenta, which when young bears sporangia in all stages of development. The sporangium originates from a single superficial cell and projects as a hemispherical papilla, which is cut off from the mother cell by a transverse wall. The lower cell takes no further part in the development of the sporangium. The first wall in the sporangial cell may be either transverse or, more often, oblique. In the latter case this oblique wall is followed by two similar ones, the three meeting so as to enclose a pyramidal apical cell, from which a varying number of segments are cut off, forming three series, the lower ones contributing to the three-rowed stalk of the sporangium. The upper ones merge somewhat gradually into the enlarged apical region of the sporangium—the capsule. The apical growth of the sporangium is stopped by the formation of a periclinal wall in the apical cell. At this stage the capsule shows a central tetrahedral cell enclosed by a single layer of peripheral cells—forming the wall of the capsule. From each face of the cen-

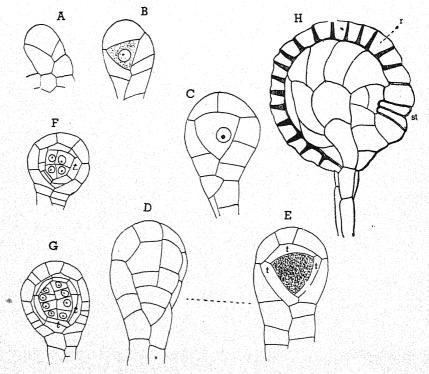


Fig. 201.—A-G, development of the sporangium in Polypodium falcatum; t, tapetum; H, mature sporangium; r, annulus; st, stomium.

tral tetrahedral cell a segment is cut off, leaving a central tetrahedral cell, the archesporium, surrounded by four primary tapetal cells.

The capsule wall remains permanently a single cell layer. The primary tapetal cells divide repeatedly and finally form a double layer surrounding the central archesporium. This divides into two equal cells and these divide into equal quadrants or octants. In most of the Polypodiaceae there are finally sixteen spore mother cells. Soon after the number of mother cells is complete the walls of the tapetal cells disintegrate and the cytoplasm and nuclei are disposed through the central region of the capsule, completely surrounding the spore mother cells, which float free in the protoplasmic mass which fills the greatly enlarged sporangial cavity. It is evident that this nucleated protoplasm, with which the included sporogenous cells are in close contact, plays an important role in the nutrition of the developing spores, including the formation of the outer protective spore membrane, the epispore. Each spore mother cell finally undergoes the characteristic tetrad division.

The sporangium wall shows a very definite arrangement of the cells. On one side of the young sporangium a special cell divides transversely into four narrow cells, the two median ones marking the place where the sporangium is to open. This apparatus is the "stomium." Joining the stomium above, and continued over the top of the capsule, is a band of narrow cells, the "annulus." As the sporangium ripens, the inner and radial walls of the annulus cells become strongly thickened and the sto-999 mium cells show a similar condition. The thickened walls of the annulus cells are highly hygroscopic. As the ripe sporangium loses its moisture the annulus contracts and acts like a spring stretched over the top of the sporangium and pulling on the stomium. This results in a split between the stomium cells, which extends laterally until the sporangium wall is almost completely divided and the cleft extends as far as the annulus. The annulus straightens out, carrying with it the upper half of the capsule, with the included spores. This movement may continue until the two ends of the annulus are almost in contact, when with a sudden jerk, as if by a sling, the spores are violently discharged.

The gametophyte.—With a few exceptions the gametophytes of the homosporous Leptosporangiatae are much alike. In the Polypodiaceae the gametophyte or prothallium is a liverwort-like, prostrate thallus, heart-shaped in outline. From the ventral face numerous rhizoids fasten the gametophyte to the substratum. At first the thallus is composed of a single layer of cells; but later a thickened cushion of cells, like that in the Marattiaceae, is developed on the ventral side back of the growing point. The archegonia are confined to this cushion.

The ripe spores most commonly have no chlorophyll; but sometimes,

e.g., in Onoclea, chlorophyll is present, and such spores germinate more quickly than those from which it is absent. In the latter, as in the Marattiaceae, chlorophyll is developed before any cell division, and results in two cells of unequal size, the larger one containing most of the chlorophyll and the smaller one elongating rapidly and forming the first rhizoid. The larger cell, as it grows, ruptures the outer membrane of the spore and as it elongates is divided by a series of transverse walls into a short filament. In the terminal cell there soon are formed two intersecting walls cutting out a two-sided apical cell, and the gametophyte becomes a broad

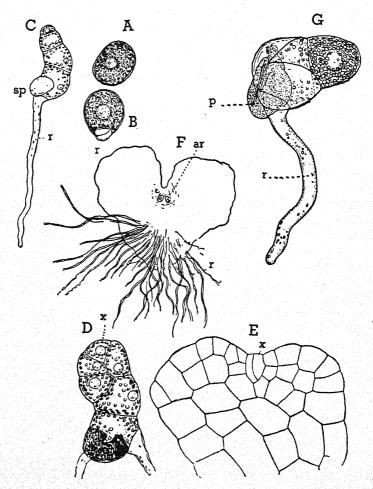


Fig. 202.—Spore germination and young gametophytes of Onoclea Struthiopteris; z, apical cell; r, rhizoid; ar, archegonia; sp, spore coat; p, outer spore membrane.

spatulate thallus. By the more active growth of the lateral segments of the apical cell the growing point occupies an indentation between the wings of the thallus, which thus becomes the characteristic heart-shaped prothallium of the common ferns. The single apical cell of the young prothallium is later replaced by a series of marginal initials, and this change is followed by the formation of the archegonial cushion. The apical growth at this stage is much like that in the Marattiaceae, and recalls that of some liverworts, e.g., *Pellia* and *Dendroceros*.

In most of the leptosporangiates archegonia and antheridia are borne on the same thallus; but it is common to encounter very small prothalli, sometimes reduced to a short filament, which bear only antheridia. More rarely normal prothallia are dioecious, as they are in *Equisetum*. Onoclea and is a notable example; but here, too, as in *Equisetum*, exceptions to the rule may occur.

Differing more or less from the Polypodiaceae in the structure of the gametophyte are several genera belonging to what are generally believed to be the more primitive families. Among these may be cited Osmunda, Gleichenia, Schizaea, Trichomanes, and Hymenophyllum. Osmunda and some species of Gleichenia have relatively large prothallia, with a massive midrib, recalling some of the thallose liverworts and also the massive prothallia of the Marattiaceae. In Schizaea the gametophyte is a branching filament, somewhat resembles a moss protonema or an alga. This is perhaps an adaptation to a semiaquatic habitat. In some species of Trichomanes a similar filamentous habit is found. In Hymenophyllum, representing the "filmy ferns," the gametophyte is a large, irregularly branching thallus consisting of a single layer of cells throughout and capable of apparently unlimited propagation by budding.

Gametangia.—The antheridia usually begin to form before the archegonia. They may be formed both above and below, or on the margins of the prothallium; but the archegonia are confined to the ventral side of the thallus. In the Polypodiaceae they are restricted to the cushion back of the growing point, but in Osmunda and Gleichenia they are formed upon the flanks of the midrib.

The antheridia show considerable variation in the different families, especially in the number and arrangement of the peripheral cells. Unlike the Eusporangiatae, however, in the Leptosporangiatae the antheridium projects entirely above the surface of the thallus and resembles superficially more nearly the Psilotaceae than the eusporangiate ferns.

Antheridium.—In the Polypodiaceae the young hemispherical antheridium mother cell is formed by a transverse wall in a superficial cell. The first wall formed in the mother cell is generally funnel-shaped, with the upper rim in contact with the outer wall of the antheridial cell and the

tip of the funnel in contact with the basal wall of the antheridium. The latter now consists of a ring-shaped basal cell and the upper funnel-shaped one. In the upper cell there is next formed a dome-shaped wall concentric with the outer wall of the antheridium. A third wall cuts off a cap-cell, and the antheridium now consists of a central cell enclosed in three peripheral cells—two lower ring-shaped ones, and the terminal cap-cell. From the further divisions of the central cells the spermatocytes are formed.

The development of the spermatozoids is much like that of *Equisetum* and the eusporangiate ferns. The nucleus of the spermatozoid is more elongated than in the latter but otherwise is very similar.

Archegonium.—The young archegonium of the leptosporangiates is much like that of the Marattiaceae. The mother cell divides into three superposed cells, the other one by a quadrant division producing the four

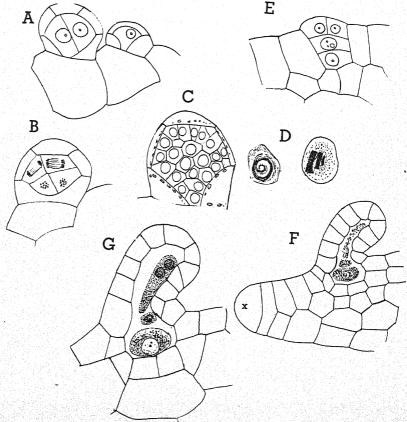


Fig. 203.—A-C, development of the antheridium in Onoclea Struthiopteris; D, young spermatozoids; E, young archegonium; F, G, mature archegonia.

cell rows of the neck. This is longer than in the Marattiaceae; and in the Polypodiaceae the two anterior rows grow faster, so that the neck is bent backward. In the Osmundaceae the four rows are alike and the neck is straight. In all of the ferns that have been investigated there is a conspicuous ventral canal cell. There may be a division of the neck canal cell into two definite cells or the division may be confined to the nucleus.

Fertilization.—As the archegonium opens and discharges the remains of the canal cells, this discharged matter exercises an attractive influence (chemotaxis) upon the free spermatozoids, which penetrate the neck and reach the venter containing the ovum. Pfeffer has shown that malic acid is present and is the direct chemotactic substance in the ferns. A very complete study of fertilization in Onoclea was made by Shaw. He states that after a spermatozoid has entered the egg, the latter loses its turgidity and no more spermatozoids can enter it. The spermatozoid penetrates the egg nucleus and for a considerable time can be easily recognized. Finally the chromosomes separate and mingle with those of the egg, which thus becomes diploid. After fertilization is complete the egg develops a cell wall, increases somewhat in size, and after a period of rest-several days in Onoclea—undergoes its first division into the two-celled diploid embryosporophyte. After fertilization is effected the tissue surrounding the embryo begins active growth and forms the calyptra, enclosing the embryo until the cotyledon and the root are well advanced.

The embryo.—The early cell divisions in the embryo of the Leptosporangiatae are much more regular than in the eusporangiates. This is

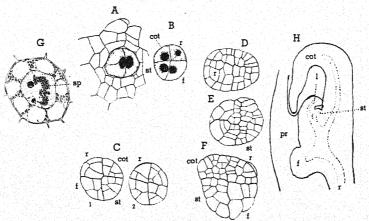


Fig. 204.—A, two-celled embryo of Onoclea Struthiopteris; B-F, development of the embryo; cot, cotyledon; r, root; f, foot; st, stem; G, egg cell of Onoclea sensibilis, fourteen hours after the penetration of the spermatozoid, sp; H, section of young sporophyte of Onoclea Struthiopteris, still attached to the gametophyte, pr, showing the arrangement of vascular bundles (G, after Shaw).

especially marked in the Polypodiaceae. In these the basal wall is vertical and nearly coincident with the axis of the archegonium, instead of transverse, as it is in the eusporangiates. The next walls are at right angles to the basal wall; and the embryo consists of four equal quadrants, which determine the four primary organs of the young sporophyte, viz., cotyledon, stem apex, root, and foot. Each quadrant is divided by a median wall into equal octants. For a brief period each octant shows a definite apical growth, segments being cut off in regular succession parallel with the inner walls of the octant, which may be said to function as a tetrahedral apical cell.

In the root quadrant the octant wall is somewhat oblique and the larger octant becomes at once the definitive apical cell of the primary root which is thus exogenous in origin instead of developing at a later period from the inner tissues of the embryo as it does in the Eusporangiatae. Of the eight original octants, one in each quadrant persists as the apical cell, respectively, of the cotyledon, the stem apex, the root, and the foot; but in the last the apical growth is soon obliterated. In the stem quadrant one of the octants becomes the permanent apical cell of the shoot and the other gives rise to the second leaf.

Cotyledon.—The apical cell of the cotyledon retains for some time its tetrahedral form and the young cotyledon has a conical form; but later the growth is from a two-sided apical cell and the terminal portion of the young leaf becomes a spatulate lamina clearly marked off from the slender petiole. As the lamina grows there is a dichotomy which is usually repeated so that the cotyledon is fan-shaped with definite dichotomous venation. The cotyledon thus closely resembles that of most of the Marattiaceae. The young cotyledon is bent forward over the stem apex and second leaf. The stem apex remains short but is more conspicuous than in corresponding stages in the Marattiaceae. The second leaf develops from the second octant of the quadrant, but like the cotyledon may be looked upon as quite independent of the stem apex. Instead of growing through the tissue of the gametophyte, as it does in the Marattiaceae, the cotyledon emerges on the lower side of the prothallium and grows upward between the two wings.

The primary root.—The earlier segments of the apical cell of the primary root are all derived from the lateral faces of the tetrahedral cell; but soon, by a periclinal wall, a cap cell is cut off from the outer free face. The subsequent growth of the root is like that in the later-formed roots. As a rule the root emerges before the cotyledon and attaches the young sporophyte to the ground.

The foot.—In the two octants forming the foot of the embryo there is no regularity in the succession of the cell divisions except in the very

earliest stages, and the foot is a conspicuous hemispherical mass composed of uniform cells embedded in the tissue of the gametophyte.

All of the organs of the young sporophyte are differentiated at a much earlier period than in the Eusporangiatae and the cell divisions are much more regular—in short, the embryo is much more specialized than that of the Eusporangiatae.

The differentiation of the vascular bundles begins shortly before the emergence of the cotyledon and root. In each of these organs an axial strand of procambium is developed, the two uniting in the center of the embryo. There is also a short branch ending blindly in the foot; and another procambium strand extends toward the stem quadrant, but whether this belongs to the stem or marks the stele of the second leaf which is still hardly visible is not clear and further investigation of this point is necessary to determine whether, as in the Marattiaceae, the stele of the axis in the young sporophyte is composed exclusively of leaf traces or whether there is a true cauline stele.

The first tracheary tissue appears at the junction of the procambium strands. In the petiole of the cotyledon the protoxylem consists of a central group of small spiral tracheids from which the development of the large metaxylem proceeds centrifugally. The phloem is poorly developed and the presence of sieve tubes is doubtful; nor can an endodermis be certainly demonstrated.

The stele of the axis is much like that of the cotyledon, but all the parts are better developed.

The primary root is monarch. The second root is formed endogenously and is situated close to the junction of the bundles of the cotyledon and the axis. As the sporophyte grows and new leaves are developed, the solid stele of the early stages is replaced by an open-meshed "dictyostele" like that in Ophioglossum and the Marattiaceae. In a young plant of the ostrich fern (Onoclea struthiopteris) a cross section of the axial cylindrical stele showed a central pith surrounded by a zone of tracheary tissue, outside of which was a zone of phloem bounded by a definite endodermis. Whether this "siphonostele" is formed exclusively of leaf traces, or whether it is in part cauline, is not clear.

THE CLASSIFICATION

The Leptosporangiatae are sometimes regarded as embraced in a single order, Filicales, co-ordinate with the two eusporangiate orders, Ophioglossales and Marattiales. As treated in the Engler and Prantl Natürlichen Pflanzenfamilien, the Filicales are divided into suborders—Eufilicineae, including all the homosporous genera; and Hydropteridineae, distinguished by their heterospory.

Eight families of Eufilicineae are generally recognized: (1) Osmundaceae; (2) Gleicheniaceae; (3) Matoniaceae; (4) Schizaeceae; (5) Hymenophyllaceae; (6) Cyatheaceae; (7) Parkeriaceae; and (8) Polypodiaceae. The latter includes a very large majority of the species and is divided by Diels into nine subfamilies.

Bower in his comprehensive study of the ferns finds that many of the genera included in the Polypodiaceae are not sufficiently closely related to be placed in a single family, and he does not recognize the Polypodiaceae as a natural family but replaces it by several others. Of the eight families mentioned the first four are distinguished by having the sporangia developed either singly or in sori where all the sporangia are developed simultaneously. For this group Bower proposes the term "Simplices." From a study of their structure, as well as from their geological history, one may conclude that these are old types, of which, like the Marattiaceae, only a relatively small number have survived. Two other series are recognized: Marginales, in which the sporangia arise from the leaf margin, e.g., Schizaea and Hymenophyllum; and Superficiales, where the sporangia are borne on the lower side of the fronds and the sporangia are not all of the same age. To this latter belong all of the Polypodiaceae.

FAMILY 1. OSMUNDACEAE

The Osmundaceae are in several respects more like the Eusporangiatae than like the other leptosporangiates. They might be considered as a distinct order co-ordinate with the Marattiales and the Ophioglossales. Hirmer has gone still farther and proposes a special subclass—Protoleptosporangiatae—intermediate between Eusporangiatae and Leptosporangiatae.

At present about twenty species are known, with three genera—Osmunda, Todea, and Leptopteris—the latter sometimes considered to be a subgenus of Todea. Of these Osmunda is most widely distributed. O. regalis occurs in both the Northern and Southern hemispheres, having a wide distribution in Eurasia and occurring also in South Africa and South America. It is found in the eastern United States but not on the Pacific Coast; and this is true of the two other American species, O. cinnamomea and O. Claytoniana, which occur also in eastern Asia. Todea has but a single species, common in South Africa and in New Zealand and Australia. Leptopteris is confined to the Australasian region and some of the Pacific islands.

The Osmundaceae are handsome ferns with pinnate or bipinnate ample fronds. In Osmunda the stem is short and completely covered by the broad leaf bases, much as in the Marattiaceae. In Todea and Leptoteris the stem is taller—sometimes in Todea a meter in height, so that it suggests

a small tree fern. In Todea and Leptopteris the sporangia are borne on the abaxial surface of unmodified leaves, much as in the Marattiaceae, but not in definite sori. In Osmunda the sporangia are borne on special pinnae, which recall the sporangiophores of Helminthostachys or Botrychium, or some of the fossil Coenopteridales. In the cinnamon fern, O. cinnamomea, all the segments of the fertile leaf are quite destitute of a lamina and are completely covered with the crowded sporangia. In O. regalis only the terminal part of the frond is fertile, and in O. Claytoniana there are several fertile pinnae in the middle of the frond. The special fertile fronds of the cinnamon fern, completely covered with sporangia, appear in the spring before the green fronds unfold—recalling the behavior of the fertile shoots of Equisetum arvense.

The stem.—The stem in the Osmundaceae is a massive upright stock or caudex, completely covered with the persistent leaf bases, much as in the Marattiaceae. The growth is from a tetrahedral apical cell. Occasion-

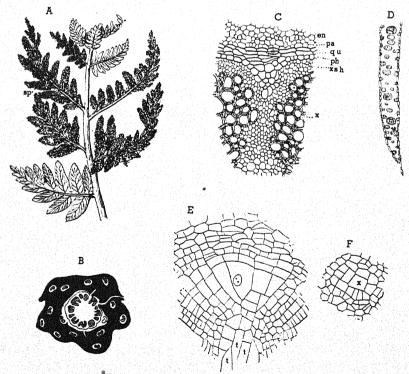


Fig. 205.—A, Osmunda Claytoniana, fertile frond; sp. sporangia; B, section of stem of O. regalis; C, part of central cylinder of the rhizome of O. regalis; D, sieve tube; E, root apex of O. cinnamomea; F, cross section of root apex of O. Claytoniana (B, after De Bary; C, D, after Zenetti).

ally there may be a dichotomy of the shoot, resulting in two equal branches. The outer cortex is composed of dark-colored sclerenchyma, the inner cortex of thin-walled parenchyma. The xylem strands form a reticulate cylinder with narrow elongated meshes, and in cross section the xylem strands form a circle of horseshoe-shaped masses surrounding the central pith from which extend medullary rays separating the xylem masses. Surrounding the xylem ring is a continuous zone of phloem with numerous conspicuous sieve tubes. Outside the phloem is the pericycle composed of several layers and the whole stele is bound by a continuous endodermis. An internal endodermis has been described by Faull in Osmunda cinnamomea and in Leptopteris hymenophylloides; but no definite internal phloem is developed.

The number of xylem strands, according to Bower, varies. In Osmunda Claytoniana there may be as many as forty, while in O. regalis there are only about fifteen and in Todea there are eight or less. In Leptopteris superba the xylem may form an unbroken cylinder. The protoxylem elements are small spiral and annular tracheids, the metaxylem larger scalariform ones like those of the typical ferns.

Bower, who has described in detail the different theories as to the nature of the stele in the Osmundaceae, concludes that in *Todea* and *Leptopteris* the structure of the stele is more primitive than in *Osmunda*. The collateral arrangement of the xylem and the phloem in the stem bundles of the Osmundaceae might be compared with that in *Botrychium*, but there is no cambium present.

The leaf.—The origin of the leaves from the growing point of the shoot is much like those of the Polypodiaceae; but the young leaf has a tetrahedral apical cell and is more conical in form, and in these respects there is a suggestion of Botrychium. The further development of the pinnate leaf is like that of the Marattiaceae and the Polypodiaceae. The structure of the lamina in Todea and Osmunda is also like that of most of the ferns and the venation is the same; but in Leptopteris the lamina is composed of only two or three cell layers, and no stomata are present. The leaf has a translucent, filmy appearance like the leaves of the Hymenophyllaceae.

The petiole in Osmunda has a single large concentric vascular bundle, crescent-shaped in section, and much like that of the Polypodiaceae but with a less definite endodermis, thus approaching the condition in the Marattiaceae. The presence of numerous mucilage cells near the bundle is also reminiscent of the latter. Another feature indicating a relationship with the Eusporangiatae is the development of conspicuous stipules, which in Todea are united by a commissure such as occurs in the Marattiaceae and the Ophioglossaceae. Bower states that such stipules are archaic



features. The chaffy scales, or paleae, so characteristic of the younger leaves in the Polypodiaceae, are absent from the Osmundaceae, but the young leaves develop hairs, sometimes in great numbers, as in *O. cinnamomea*, where the young fertile fronds are covered with thick-felted covering of hairs.

The root.—The roots of the Osmundaceae, like the leaves, are intermediate in structure between the Marattiaceae and the Polypodiaceae. While there may be a single tetrahedral apical cell, this, according to Bower, is found only in the smaller roots of O. regalis, while the larger roots of this species, and also of Todea, showed much less regularity in their apical growth. Sometimes instead of a single apical cell three or four similar prismatic initials were present both in form and segmentation. closely resembling the condition in the large roots of the Marattiaceae. In O. cinnamomea the large apical cell is a four-sided pyramid, and it is possible that the very large lateral segments sometimes assume the role of initials. The root cap is developed in part from the apical cell but also in part from the outer cells of the lateral segments as in the Eusporangiatae. Of the Osmundaceae, Osmunda Claytoniana most nearly resembles the Polypodiaceae in its root structure. The stele of the root is diarch in most cases but occasionally may be triarch—a possible approach to the polyarch bundles of the Eusporangiatae.

The sporangium. — The development of the sporangium has been studied in detail by Bower. Like the other organs it is, to some extent, intermediate between the eusporangiate and leptosporangiate types; but there may be a good deal of difference in the early divisions, even in the same species. As in the Eusporangiatae, the sporangium cannot be traced back to a single mother cell and the early stages are much like those of Botrychium or Helminthostachys. There is, however, at a very early stage, a large median cell from which the major part of the sporangium develops. This cell shows a regular segmentation very similar to that in the typical Leptosporangiatae. There is cut out a central cell which may be tetrahedral, as in the Polypodiaceae, or the inner portion is truncated, so that in section it is nearly rectangular in outline, thus resembling Botrychium.

The wall of the sporangium conforms to the leptosporangiate type, being composed of a single cell layer. The tapetum is usually double but may have three layers. On one side of the ripe sporangium is a transverse group of cells with thickened walls. This is the annulus, which is not unlike the rudimentary annulus of Angiopteris and Macroglossum. On the opposite side of the sporangium is a vertical line of narrow cells marking the position of the longitudinal cleft where the sporangium opens. The number of spores is relatively large, sometimes upward of 500 in Osmunda.

The gametophyte.—The ripe spores of Osmunda contain chlorophyll and germinate promptly, like those of Equisetum. As in the latter, the spores soon lose their viability. Within twenty-four hours the spore may show the first division. Previous to this there is usually some elongation of the cell before the first division wall is formed. This in most cases separates a small rhizoid from the large cell from which the gametophyte

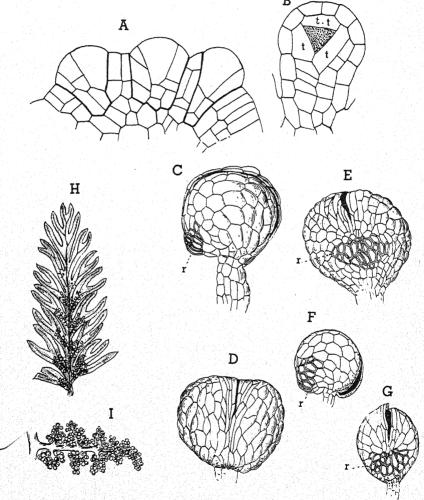


Fig. 206.—A, B, young sporangia of Osmunda regalis; t, tapetum; C-E, three views of the sporangium of O. cinnamomea; F, G, sporangia of Todea hymenophylloides; r, annulus; H, fertile pinna of T. hymenophylloides; I, fertile pinnule of Osmunda Claytoniana (A, B, after Bower).

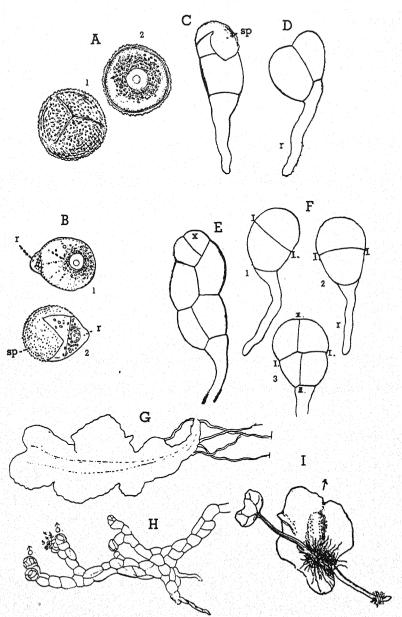


Fig. 207.—A-E, germination stages of Osmunda Claytoniana; r, rhizoid; sp, spore membrane; F, germination in O. cinnamomea; G, older gametophyte of O. Claytoniana; H, dwarf male gametophytes; I, gametophyte of O. Claytoniana, with attached sporophyte.

develops. The next steps vary a good deal and there is often a tendency to form a cell mass, as in the Marattiaceae. This tendency is more marked in O. cinnamomea and O. regalis than in O. Claytoniana, which more nearly resembles the Leptosporangiatae in the structure of the gametophyte. An endophytic mycorrhiza, like that of the Marattiaceae, has been found in O. cinnamomea.

In general the prothallium shows the heart-shaped form of the common ferns; but it is more elongated and has a massive midrib, so that it much resembles such a liverwort as *Calycularia* or *Dendroceros*. In apical growth and general structure it bears a striking resemblance to the latter. In the earlier stages there is usually present a two-sided apical cell, which is later replaced by a group of marginal initials, as in the typical Leptosporangiatae. The development of the midrib begins very early, so that in the older elongated prothallium the thickened midrib is very conspicuous.

Occasionally dichotomous branching occurs; and not infrequently small lateral branches may be formed, which may become detached and form an independent prothallium. Sometimes, especially where the prothallia are crowded, small gametophytes, often of irregular shape, are found which bear numerous antheridia but no archegonia. The archegonia are confined to the large prothallia and are borne on the flanks of the midrib on the lower side of the thallus. In O. Claytoniana an archegonial cushion like that in the Marattiaceae is formed also; but this is absent in the other species.

Gametangia.—The antheridium differs a good deal from that of the Polypodiaceae but, like it, projects free above the surface of the prothal-lium. It thus differs from the sunken antheridium of the Eusporangiatae. The early divisions in the mother cell are oblique and intersect so as to enclose a central tetrahedral cell which functions for a short time like an apical cell. Finally a cap cell is cut off from this cell, and the resulting central cell by repeated division forms the mass of spermatocytes as in the Polypodiaceae. The cap cell divides into a small group of cells, one of which is a definite opercular cell, like that in the Eusporangiatae. There are also secondary divisions in the lateral wall cells, so that the number of wall cells in the ripe antheridium is considerably greater than in the Polypodiaceae.

The archegonium is much like that of the Polypodiaceae, but it projects horizontally from the flanks of the midrib instead of vertically downward as it does in the Polypodiaceae. Associated with this, the neck is straight instead of bent backward.

The embryo.—The first (basal) wall in the zygote is in the same plane as the axis of the archegonium neck, as it is in the Polypodiaceae; but the

second (quadrant) wall is also in the plane of the archegonium axis, and not transverse as it is in the Polypodiaceae, although the relation of the quadrants of the embryo, with reference to the prothallium, is the same in the two cases; and the primary organs developed from the quadrants are arranged as in the typical fern embryo, with reference to the prothallium but not to the archegonium.

Like the Polypodiaceae the primary organs of the embryo are established by the quadrant division. Regular octant walls are also formed; but the subsequent divisions are much less constant, and in this respect Osmunda may be regarded as intermediate between Leptosporangiatae and Eusporangiatae. The differentiation of the organs occurs later than in the Polypodiaceae. The embryo retains for a much longer period its nearly globular form, and it does not emerge from the calyptra until it has reached a much greater size. These characters also recall the Eusporangiatae.

The cotyledon has a fan-shaped lamina, the result of the dichotomy of the apex—thus agreeing with the condition in most of the ferns. The vascular bundle of the petiole is nearly collateral in structure and is most like some of the Marattiaceae.

The primary root has a tetrahedral apical cell, which divides less regularly than in the Polypodiaceae and more nearly resembles that of *Botrychium*. The vascular bundle of the root is diarch. The foot is larger relatively than in the Polypodiaceae; and this agrees also with the condition in the Ophioglossaceae and the Marattiaceae.

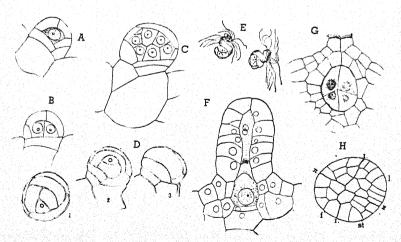


Fig. 208.—A-C, young antheridia of O. cinnamomea; D, surface views of ripe antheridium of O. Claytoniana; o, opercular cell; E, spermatozoids of O. Claytoniana; F, archegonium of O. cinnamomea; G, eight-celled embryo of O. Claytoniana; H, older embryo of same species.

RELATIONSHIPS OF THE OSMUNDACEAE

Professor Bower, in his very complete study of the ferns, believes that the Osmundaceae are the remnants of an ancient order intermediate between Eusporangiatae and Leptosporangiatae. This view is accepted by other investigators and seems to be justified.

This is borne out by the fossil record, which indicates that the order was represented in the late Palaeozoic and possibly earlier. These early records are mostly petrified stems whose structure is well preserved and agrees closely with the structure of the existing Osmundaceae. Examples of such fossil stems are Zalesskya and Thamnopteris from the Upper Permian of Russia. The leaves and sporangia of these forms are unknown; but in the Upper Carboniferous sporangia resembling those of the Osmundaceae have been found, although it is by no means certain that they really belong to the Osmundales. It is suggested that there may be a possible relationship between the existing Osmundaceae and the extinct Palaeozoic order Coenopteridales.

In the Jurassic and Lower Cretaceous are several species of "Osmundites" whose stem structure approaches very closely that of the Osmundaceae. The later forms are evidently more advanced than the earlier types from the Jurassic and Permian. There is a progression in the size and complexity of the stelar structures from the early Permian types to the late Jurassic and Cretaceous species.

Among the characters of the Osmundaceae generally accepted as primitive are: the tendency to dichotomy of the shoot apex; the stipular sheath and commissures, which they share with the Eusporangiatae; the tetrahedral apical cell of the young leaf and the indefinite character of the meristem of the root apex; and a corresponding condition in the young sporangium—also suggestive of the eusporangiates. The predominance of hairs rather than scales is also a character of the more primitive ferns.

Bower compares the marginal insertion of the sporangia on the narrow leaf segments of *Osmunda* with the sporangiophores of some of the Coenopteridales, and believes this is the more primitive condition while the transfer of the sporangia to the lower surface of the frond in *Todea* is secondary.

The large green gametophytes, which like the Marattiaceae may harbor a fungus endophyte, and the structure of the gametangia are to some extent intermediate between the Marattiaceae and the more specialized leptosporangiates. The embryo, also in its large size and long dependence on the gametophyte, approaches the eusporangiate condition.

Bower concludes: "The Osmundaceae may therefore be held to be a synthetic type connecting the Eusporangiate and Leptosporangiate Ferns."

As to their immediate relatives, Bower says: "The type is an isolated

one. There is no family of living Ferns closely related to them; but it is quite possible that as knowledge increases affinities with other Palaeozoic fossils may be drawn closer than at present recognized." He also concludes that the difference seen in the genera of the Osmundaceae, respecting the position of the sporangia, prefigures two distinct trends in the evolution of the Leptosporangiatae. These represent two types, which Bower designates "Marginales" and "Superficiales," represented among the more primitive types, respectively, by the Gleicheniaceae and Schizaeaceae.

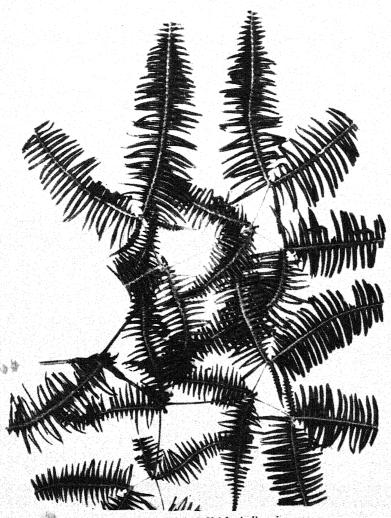


Fig. 209.-Frond of Gleichenia linearis.

GLEICHENIACEAE

The Gleicheniaceae form a very natural family, with about eighty known species, distributed through the tropics and the temperate regions of the Southern Hemisphere. None occur in the United States, but species occur in southern China and Japan. Except for the monotypic Stromatopteris moniliformis, they are usually all placed in the single genus Gleichenia, which, however, has three subgenera—Dicranopteris, Eugleichenia, Platyzoma. Bower thinks the latter should be separated as an independent genus. One species, G. linearis (= L. dichotoma) occurs throughout the tropics or subtropics of both hemispheres; the others are more restricted in their range.

The stem is most commonly a slender creeping rhizome with the leaves separated by long internodes. The rhizome may often branch dichotomously. The leaves may be simply pinnate; but in many species, e.g., G. linearis and G. glauca, they show long-continued growth and may reach a length of several meters and form dense, almost impenetrable thickets, or climb over shrubs or into trees. This long-continued independent growth of the leaves emphasizes the lack of sharp demarcation between stem and leaf.

The branching of the frond has the appearance of a repeated dichotomy; but it has been clearly shown that, although a true dichotomy may occur in a few forms, in general the forking of the frond is the result of an arrest of the growing point of the pinnate leaf and the development of two lateral pinnae, which may repeat the process indefinitely. This also can sometimes be seen in the cotyledon. In the majority of species the pinnules are flat and the sporangia are in compact, naked sori, forming a regular row parallel with the midrib of the pinnule. In other species, e.g., G. polypodioides, the pinnules are contracted and the sori are enclosed by the incurved leaf margins.

Platyzoma, a small xerophytic plant, differs greatly in habit from the other subfamilies, and Bower concludes that it should be given generic rank. The short rhizome bears two types of closely set leaves, very small, linear, sterile ones, and much larger, simply pinnate, fertile ones. The pinnae are very small and the margins are reflexed so as to cover the sori. The only species is P. microphylla from Australia.

The structure of Stromatopteris moniliformis, from New Caledonia, the only described species, is still only imperfectly known. It is said to have a subterranean rhizome from which upright forking branches are produced. On these branches the slender pinnate leaves are borne. A single small sorus is formed on each leaflet. The pinnae (or pinnules) have a conspicuous midrib from which extend the dichotomously branching lateral veins. Epidermal hairs and scales are common.

The stem.—The stem in Gleichenia has a massive central vascular cylinder with a definite endodermis. The cortical tissue is a dark-colored sclerenchyma. Within the endodermis is a pericycle of several layers surrounding a broad zone of phloem containing many sieve tubes. In most species the central portion of the vascular cylinder, the xylem, contains many large scalariform tracheids intermingled with parenchyma. Several protoxylem groups are present, but Bower calls the whole structure a protostele.

In G. pectinata the "stele" of the stem is a hollow cylinder or "soleno-stele" with both inner and outer phloem and endodermis. The stout petiole has a single, large, concentric vascular bundle much like that of Osmunda.

While the vascular cylinder in *Gleichenia* is generally considered to be a cauline "stele," and the leaf-traces are considered as derivations of it, the figures and diagrams in Bower's *Ferns* could quite as well be interpreted as indicating that the "stele" is formed as in the Marattiaceae—as the result of the fusion of independent leaf-traces.

The sporangia.—The sporangia in Gleichenia are developed on a receptacle formed when the leaf is still young. The sporangia arise from the margin of the receptacle and sometimes from the central region. The number is never very large and all are formed simultaneously. As in Osmunda it is difficult to trace the sporangium back to a single mother cell. The development is very much like that in Osmunda, and a tetrahedral archesporium is present from which the tapetal cells are cut off. The tapetum is double, the inner cells becoming much enlarged and multinucleate, recalling in this respect the tapetum of Angiopteris. There is a

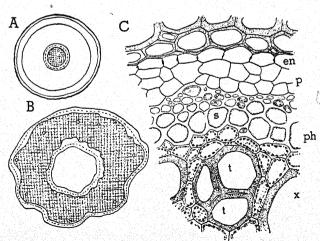


Fig. 210.—A, diagram of tissues of the rhizome of Gleichenia flabellata; B, similar diagram of G. pectinata; C, details of vascular bundle in G. linearis (all figures after Boodle).

certain similarity in the arrangement of the sporangia in the sorus of Gleichenia and the synangia of the Marattiaceae.

The sporangia are pear-shaped with a very short, thick pedicel. There is a complete annulus, composed of a single row of large, thick-walled cells

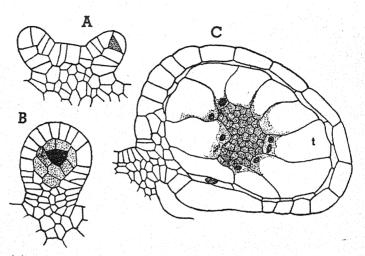


Fig. 211.—Development of the sporangium of G. flabellata (after Bower).

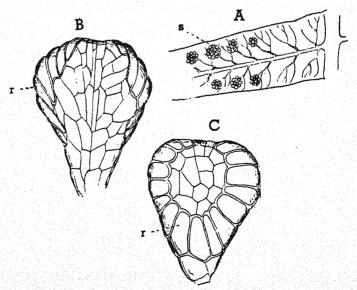


Fig. 212.—A, pinnule of Gleichenia linearis, with sori, s; B, C, two views of ripe sporangium; r, annulus.

forming an oblique plate interrupted at the apex of the sporangium by several thin-walled cells, from which extend two rows of narrow cells; and between these is the vertical slit by which the sporangium opens as it does in Osmunda. The complete annulus is more like that of the typical Leptosporangiatae.

As in the Osmundaceae, the number of spores in the Gleicheniaceae is larger than in the typical leptosporangiates and recalls the condition in the Eusporangiatae. Bower found the highest number (838) in G. fla-

bellata.

Gametophyte.—The gametophyte in Gleichenia shows considerable variation. In the species of Dicranopteris, e.g., G. pectinata and G. linearis,

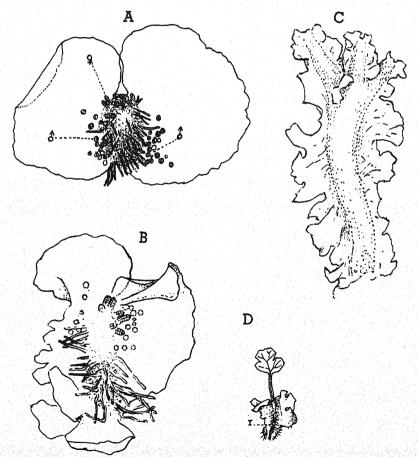


Fig. 213.—A, gametophyte of Gleichenia polypodidioides; \mathcal{C} , archegonia; \mathcal{C} , antheridia; \mathcal{C} , ventral view of gametophyte of \mathcal{C} . pectinata, showing gametangia; \mathcal{C} , old gametophyte of \mathcal{C} . linearis; \mathcal{C} , young sporophyte of \mathcal{C} . pectinata, attached to the prothallium; \mathcal{C} , root.

it resembles the prothallium of Osmunda regalis or O. cinnamomea, having a very conspicuous midrib upon which the archegonia are formed. In G. laevigata and G. linearis the much-elongated prothallium has a very thick midrib and marginal folded lobes, so that it resembles a liverwort like Fossombronia or Dendroceros. In G. polypodioides, belonging to Eugleichenia, the short broad prothallium is very much like that of the Polypodiaceae and there is a definite archegonial cushion, the midrib being much less prominent. In all of the species examined an endophytic mycorrhiza, like that in the Marattiaceae and Osmunda, is found in the older parts of the gametophyte. Dichotomy may occur in the large prothallia.

Gametangia.—The antheridia usually are restricted to the ventral surface of the prothallium, both on the thin wings or on the flanks of the midrib, less commonly mixed with the archegonia. The latter at first are

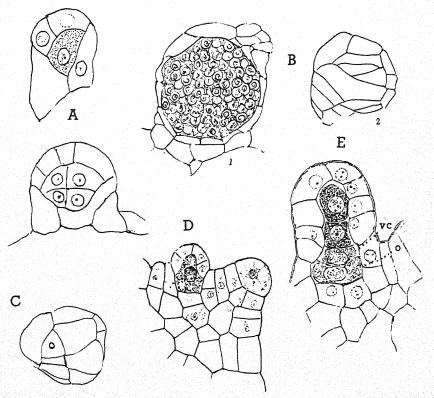


Fig. 214.—A, young antheridia of Gleichenia pectinata; B, median section of ripe antheridium of G. laevigata; B, 2, surface cells of the same; C, surface view showing opercular cell; D, apex of gametophyte of G. pectinata, with young archegonium; E, older archegonium of the same.

formed on the cushion near the apex as in the Polypodiaceae; but in the larger prothallia they are restricted mainly to the flanks of the midrib, resembling *Osmunda* in this respect. In *G. laevigata* the antheridia may also occur on the dorsal surface of the prothallium.

The antheridium shows a good deal of difference between some of the species. In Dicranopteris, e.g., G. pectinata and G. laevigata, the antheridium resembles that of Osmunda; in G. polypodioides (sec. Eugleichenia) it is much smaller, and more like that of the Polypodiaceae. In G. pectinata there are about twelve parietal cells and in G. laevigata a still larger number. As in Osmunda and the Eusporangiatae, there is a definite opercular cell. The number of spermatozoids is greater than in any other of the Leptosporangiatae—several hundred in G. laevigata.

The neck of the archegonium may be straight, as in Osmunda, or it may be bent; but instead of bending backward as it does in the Polypodiaceae it is bent forward. There are often two distinct neck canal cells, but sometimes the division wall is not formed.

The embryo.—The first divisions of the embryo are like those in the Polypodiaceae. The epibasal region develops the cotyledon, the hypobasal the foot and root. The foot is larger than in the Polypodiaceae and thus suggests Osmunda or the Marattiaceae; but the root is sometimes, at least, derived at once from one of the hypobasal quadrants, as it is in Osmunda and the Polypodiaceae; but it is possible that the apical cell of the root may sometimes be formed endogenously, although the root does not penetrate the foot as it does in the Marattiaceae and the foot remains as a conspicuour haustorium like that in other leptosporangiate ferns. The cotyledon emerges on the lower side of the prothallium and soon pushes up between the wings and grows vertically upward. As the cotyledon and root emerge their axes are nearly in the same plane and a section of the young sporophyte resembles that of the Marattiaceae except for the conspicuous foot. The stem apex is inconspicuous but shows a very definite tetrahedral apical cell. As the vascular bundles are differentiated, the steles of the root and cotyledon are continuous, as they are in the Marattiaceae. Whether or not a cauline stele is developed is not certain, but it is not impossible, judging from some sections that have been examined. In other cases there seemed to be no cauline stele developed. In order to decide this point further investigation is necessary. The young cotyledon shows the characteristic circinnate curvature. The second leaf can be recognized about the time the cotyledon emerges.

The development of the permanent tissues of the vascular bundles begins near the junction of the young bundles. The primary tracheids are reticulate.

The young cotyledon approximates the flabellate form of the typical

ferns, but it is not easy to determine whether or not there is a true dichotomy. Sometimes there is apparently an unequal dichotomy, the larger segment developing into the apex of the pinnate first leaf. In other cases the growth seems to be really apical and the two lobes of the young cotyledon are really lateral organs. In either case there is a prolonged apical growth of the cotyledon similar to that characteristic of the later leaves of the larger species of *Dicranopteris*.

The structures of the vascular bundles of the young axis and the petiole of the cotyledon are essentially the same as in the adult sporophyte.

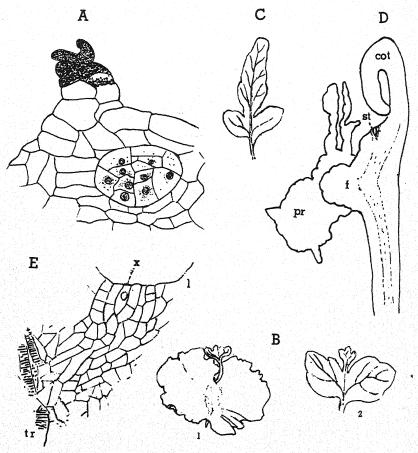


Fig. 215.—A, archegonium of Gleichenia pectinata containing a young embryo; B, young sporophyte of G. linearis, attached to gametophyte; B, 2, an older cotyledon of the same; C, full grown cotyledon; D, median section of a sporophyte of G. linearis, still attached to the gametophyte, pr; cot, cotyledon; st, stem apex; f, foot; E, stem apex of G. linearis; x, apical cell; l, cotyledon; tr, primary tracheids.

FOSSIL GLEICHENIACEAE

According to Bower the oldest undoubted Gleicheniaceae are from the Triassic, and throughout the later Mesozoic there is a very general distribution of the family, some occurring as far north as Greenland. Some Carboniferous genera, e.g., Oligocarpia, have been assigned provisionally to the family, but their relationship is problematical.

RELATIONSHIPS OF THE GLEICHENIACEAE

The Gleicheniaceae are evidently all closely related. The prevalence of dichotomy in the stem and the long-continued growth of the leaf apex indicate how vague is the distinction between shoot and leaf. Bower notes the prevalence of the "protostele" as indicative of the relatively primitive character of the family. The marked exception to this, the "solenostele" of *G. pectinata*, he thinks is sufficient to make this species the type of a subgenus—*Eudicranopteris*.

Bower concludes that *Dicranopteris* is the most primitive subgenus. This is based upon the ample "pecopterid" pinnules, the protostelic axis, and the uniseriate sori with large spore output. To this might be added the large gametophyte and the numerous spermatozoids. *Eugleichenia*, with the contracted pinnae, with a single sorus and few sporangia with a smaller spore output, is explained as a xerophytic derivative of the *Dicranopteris* type. The gametophyte is smaller and the antheridia approach more nearly the Polypodiaceae, admittedly a more modern group.

Stromatopteris and Platyzome are also considered to be specialized xerophytes most nearly related to Eugleichenia.

In regard to the structure and position of the sporangia a comparison might be made with the Osmundaceae, especially *Todea*, or even with the eusporangiate Marattiaceae. In another direction there is a marked resemblance to the leptosporangiate families, Cyatheaceae and Matoniaceae. The structure of the gametophyte and embryo of the Gleicheniaceae is also intermediate in character.

CHAPTER XVI

LEPTOSPORANGIATAE: MATONIACEAE, DIPTERIDACEAE, SCHIZAEACEAE, HYMENOPHYLLACEAE

MATONIACEAE

This small family contains but three known species from very restricted areas in the Malayan regions. The best-known species is *Matonia pectinata*, a very handsome plant with large fan-shaped fronds borne on stiff stipes sometimes two meters in height. The frond is divided into two equal parts, each of which by repeated unequal dichotomy consists of a rachis bearing a regular series of pinnatifid leaflets. The whole frond resembles a large flabellate *Gleichenia*. The leaves arise singly from an elongated, dichotomously branched rhizome.

M. sarmentosa, known only from a single Bornean locality, differs greatly in appearance from M. pectinata. The writer visited the limestone caves in Sarawak where the plant grows. The rhizomes are attached to the wall of the caves and the long pendent leaves have a slender stipe and ribbon-shaped, dichotomously divided pinnae.

The structure of the rhizome in *M. pectinata* resembles that of *Gleichenia pectinata*, but within the "solenostele" is a second cylindrical stele and a central solid vascular cylinder. In *M. sarmentosa* there is a single solenostele and a central solid cylinder. The tissues of the leaf in *Matonia* are much like those of *Gleichenia*.

The sessile sporangia of *Matonia* form a compact sorus much like that of *Gleichenia*, but there is also a conspicuous, umbrella-like indusium, developed from the central receptacle. The sporangia in their development resemble *Gleichenia*; but the annulus and dehiscence, which is transverse, recall the sporangia of the Cyatheaceae.

Very little is known about the gametophyte, which probably is not very different from that of *Gleichenia*. Bower states that "the cotyledon is either simple or branched and its venation is a scorpioid sympodium as it is in *Gleichenia*."

Fossils.—The few existing species of Matonia are evidently relicts of a group of ferns which played an important role during the Mesozoic from the Upper Triassic through the Jurassic and Cretaceous. In the latter formations the living M. pectinata, or a closely related species, has been discovered. Laccopteris and Matoniadium are widespread Mesozoic genera showing a close resemblance to the living Matoniaceae.

Relationships.—Bower in his study of the Matoniaceae concludes from a comparison of the Matoniaceae and Gleicheniaceae that the former represent a specialized type which at an early period—perhaps in the Triassic—diverged from the same stock as the Gleicheniaceae. A study of the stelar structures shows that most of the species of Gleichenia have a simpler structure than Matonia; but the highly specialized stele of Matonia pectinata is connected with the simple Gleichenia-type through Platyzoma and G. pectinata. The sporangium of Platyzoma also is most like that of Matonia.

Seward believes that the generic type *Matonia* originated in the Northern Hemisphere in Triassic or early Jurassic time, reaching its culmination

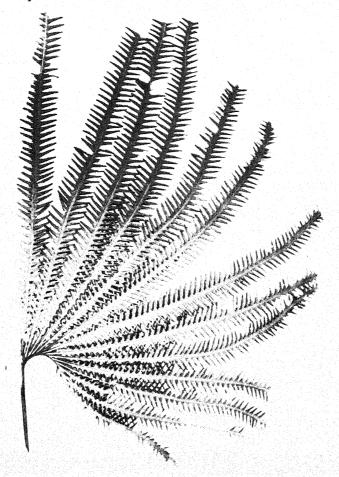


Fig. 216.—Leaf of Matonia pectinata (photograph by Mr. John Poindexter).

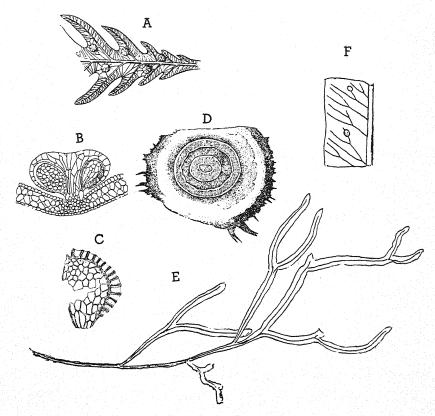


Fig. 217.—A, base of fertile pinna of *Matonia pectinata*; B, section of sorus of the same; C, open sporangium; D, section of rhizome; E, *Matonia sarmentosa*; F, veins and sori from fertile leaf (A, B, after Diels; D, after Seward; F, from Bower, after Diels).

in the Mesozoic era, after which it declined until its present extremely restricted distribution indicates approaching extinction.

DIPTERIDACEAE

Often growing with Matonia pectinata is another striking fern, Dipteris conjugata, the tall stipes of which, bearing broad bifid fronds, suggest a possible relationship with Matonia. The two divisions of the fan-shaped frond have the margin deeply cut but not divided into complete segments. The primary veins are dichotomous, but between them is an extensive system of secondary reticulate veins. The numerous circular sori are scattered over the lower surface of the frond. The leaves, which are arranged much as in Matonia, arise from a prostrate rhizome, which is covered with coarse hairs. The structure of the rhizome is like that of Gleichenia pectinata, the axial bundle being a hollow cylinder or solenostele.

Five species of *Dipteris* are recognized, mainly confined to the Indo-Malayan region; but one species occurs in China, and *D. conjugata* also is found in some of the Polynesian Islands—e.g., Samoa and Fiji. In some species, e.g., *D. Lobbianum*, the dichotomous character of the leaf is more conspicuous and the narrow leaf segments are almost completely separated. In this species, also, the sori approach the linear arrangement of *Matonia* or *Gleichenia*.

Sporangia.—The sori have no indusium, thus resembling Gleichenia. As in the latter, the sporangia of a sorus may all be of like age, or sometimes, e.g., in D. conjugata, the sorus may be of the "mixed" type characteristic of the Polypodiaceae. The oblique annulus is like that of Gleichenia lineata, but the sporangium opens transversely as it does in Matonia and the Polypodiaceae. The young sporangium, according to Bower, grows from a two-sided apical cell, while in most ferns it is tetrahedral. The two-sided apical cell is also found in the young sporangium of the Cyatheaceae.

Bower figures a prothallium of *D. conjugata* collected by Professor W. H. Lang; but no account of the structural details is available. The figure closely resembles the gametophyte of *Gleichenia laevigata*.

Fossils.—Like Gleichenia and Matonia the Dipteridaceae were evidently abundant and widespread during the Mesozoic. In the Rhaetic and early Jurassic there were several genera, e.g., Dictyophyllum and Hausmannia, which were apparently related to Dipteris. These became less numerous in the later formations. Seward says: "There is good reason to suppose that this alliance, viz., Matonia, Dipteris, was no more widely distributed in Tertiary floras than it is at the present day."

Relationships.—Bower concludes that while the Dipteridaceae may be regarded as related to the Gleicheniaceae and the Matoniaceae, they have not been derived directly from either family. The Matoniaceae and Dipteridaceae perhaps represent independent lines of specialization from a stock related to the Gleicheniaceae and the inclusion of Dipteris in the Polypodiaceae, because of the scattered naked sori, does not seem to be warranted. With increasing knowledge of the Mesozoic ferns and a more complete investigation of some existing genera which show indications of relationship with Dipteris, it seems very probable, as Bower believes, that a considerable number of so-called Polypodiaceae are descendants of some Dipteroid type. Among these Dipteroids Bower includes the genera Cheiropleura and Platycerium. These Bower suggests are derivatives of the Dipteris line, in which the naked superficial sori never developed a protective indusium.

SCHIZAEACEAE

The Schizaeaceae, with about one hundred species, are, like the Matoniaceae, apparently related to certain fossil types of the Mesozoic and pos-

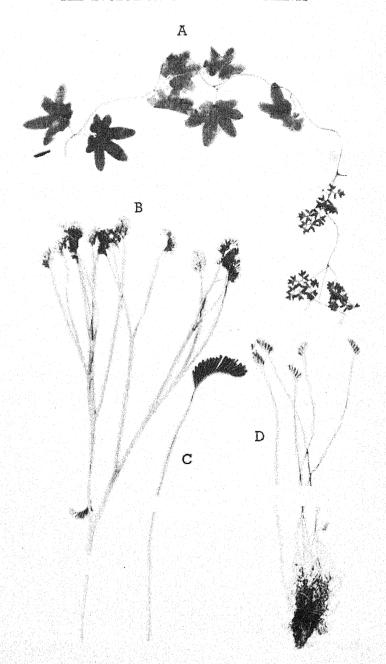


Fig. 218.—A, Lygodium palmatum; B, Schizaea dichotoma; C, fertile leaf of S. bifida; D, S. pusilla (photographs by Mr. John Poindexter).

sibly of the Palaeozoic. Sporangia of Senftenbergia, from the Carboniferous, have been referred to the Schizaeaceae, although this attribution has been questioned. Klukia, from the Jurassic, according to Bower, certainly belongs to this family.

At present they are widespread in the warmer climates and a number of species are found in the temperate zones, especially in the Southern Hemisphere. In North America Schizaea pusilla is found in New Jersey, Newfoundland, and Nova Scotia; and the climbing fern, Lygodium palmatum, occurs from Florida to Massachusetts. Species of Anemia are found in Florida and Texas.

The largest genus, Anemia, except for two African species, is confined to America. Schizaea and Lygodium are cosmopolitan, while the monotypic Mohria caffrorum is confined to South Africa. Some of the smaller species, e.g., Schizaea pusilla and Anemia elegans, are delicate plants with leaves only a few centimeters long. The largest are species of Lygodium in which the slender twining leaves have a long-continued apical growth and may reach a great length. The leaves of L. articulatum, a New Zealand species, are said to reach an extreme length of 50 to 100 feet.

The other genera are for the most part plants of moderate size with short upright stems bearing spirally placed leaves. In *Lygodium* there is a prostrate, dichotomously branched rhizome with leaves arranged in two alternate dorsal series, which are close together.

Rhizome.—The rhizome in Lygodium has a solid central cylinder (protostele—Bower) consisting of a core of xylem, surrounded by phloem, pericycle, and endodermis. This might perhaps be called a simple concentric bundle. The petiole has a similar axial bundle. Considering the great development of the leaf, it might be questioned whether the stele of the rhizome is not entirely made up of the leaf traces.

In young plants of Schizaea and Anemia, according to Bower, the stele has a solid core of tracheids but no parenchyma, and the structure of the bundle is much like that in the rhizome of Lygodium. As the stem increases in size there is developed in the stele a central mass of phloem within the xylem, and in still more advanced stages the xylem forms a ring surrounding the central pith—a solenostele. Bower's figure (The Ferns, Fig. 443) suggests that this ring of tracheary tissue is made up from the union of the leaf traces, closely resembling similar stages in Botrychium and Kaulfussia; and it is quite likely that the vascular cylinder or stele of the shoot is not of cauline origin but the result of the fusion of leaf traces as it is in the Eusporangiatae.

In Anemia hirsuta the tubular stele encloses a medulla composed of "sclerenchyma." The stele has an outer and inner endodermis—pericycle and phloem.

In most species of Anemia and in Mohria, the vascular bundles of the stem form a more or less definite dictyostele, like that of the typical Leptosporangiatae. Like the stem bundles, those of the petiole and larger veins are also concentric; but in Schizaea, according to Prantl, except for the stem bundles, they are all collateral, as they are in Ophioglossum. In most of the Schizaeaceae the cortical tissues of the stem and petioles are mainly sclerenchyma.

The leaf.—In Schizaea pusilla the sterile leaves are very slender with no trace of a lamina. The fertile fronds are longer and bear at the apex a "sorophore," a pinnate structure composed of about five pairs of narrow segments. In S. dichotoma and S. bifida, the frond is dichotomously divided, but the divisions are very narrow and have a single median vascular bundle. In the fertile frond each division bears a sorophore like that of S. pusilla.

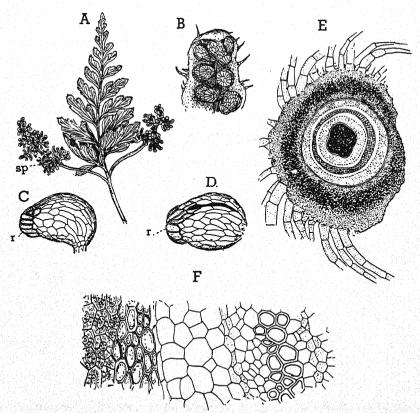


Fig. 219.—A, frond of Anemia hirsuta; sp, the fertile pinnae; B, segment of fertile pinna, enlarged; C, D, sporangia; r, annulus; E, section of rhizome; F, part of central region of rhizome.

In other genera the leaves are pinnate, but there are modified pinnae upon which the sporangia are borne. In Lygodium, as already stated, there is a continuous growth of the leaf apex something like that in Gleichenia, and the slender rachis of the leaf twines about its support like the stems of so many climbing plants. According to Prantl the formation of the pinnae is by a repeated dichotomy of the leaf apex; one division continues its growth, the others forming a pinna. The venation is dichotomous, but there may be a definite midrib in the large leaf segments. In Anemia the mother cell of a stoma is cut out by a circular wall, so that the stoma occupies the center of an epidermal cell. The epidermal appendages are mostly hairs. Only in Mohria are scales (paleae) present.

The fertile pinnae of Lygodium are usually much contracted and sometimes, e.g., in L. palmatum, the whole terminal portion of the frond is composed of the fertile pinnae. In other cases, e.g., L. Japonicum, the fertile pinnae are much like the sterile ones, the sporangia being restricted to small marginal sorophores. In Anemia the two lower pinnae have greatly elon-

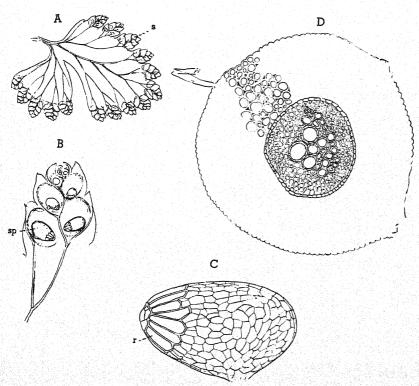


Fig. 220.—A, fertile leaf segment of Lygodium japonicum; s, sorophore; B, section of a sorophore; C, sporangium; r, annulus; D, cross section of the petiole.

gated stalks and the lamina is more divided than in the sterile pinnae. In *Mohria* there is little difference between the fertile and sterile leaves except that the margins of the former are bent under so as partly to cover the marginal sporangia.

The sporangium.—The development of the sporangium in the Schizaeaceae shows certain resemblances to the Osmundaceae and to Botrychium. The sporangia develop from the margin of the fertile leaf segments (sorophores), and as in the Osmundaceae are to some extent intermediate between the eusporangiate and leptosporangiate type. The sporangia arise in acropetal succession from the young sorophore. Special marginal cells mark the position of the young sporangium, but the adjacent marginal cells also contribute in part to the base of the young sporangium. A series of intersecting walls are formed, finally resulting in a central tetrahedral cell like that in the typical Leptosporangiatae. From the central tetrahedral cell is first cut off, by a periclinal wall, the cap cell or primary wall cell by repeated divisions from which the major part of the sporangium wall, including the annulus, is developed. The tapetum becomes double, sometimes three-layered. In Lygodium the tapetal cells may be binucleate and the outer layer remains intact. The annulus in the Schizaeaceae is very characteristic. It is a ring of thick-walled cells at the apex

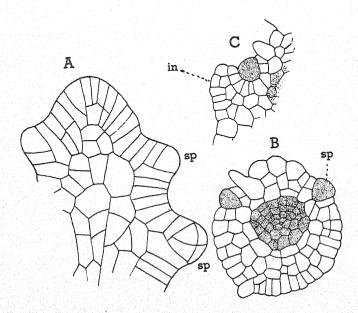


Fig. 221.—A, apex of young fertile leaf segment of Anemia Phyllitidis; sp, young sporangia; B, cross section of young sorophore of Schizaea pennula; C, young sporangium and indusium, in (all figures after Prantl).

of the sporangium. Within the annulus is either a single thin-walled cell (Schizaea, Lygodium) or, e.g., in Anemia and Mohria, a "plate" composed of several cells. Dehiscence is by a vertical cleft, as in Osmunda and Gleichenia.

In Anemia and Mohria the active growth of the adjacent tissue pushes the marginal sporangia to the lower surface of the sorophore and forms a sort of continuous marginal indusium. In Lygodium each sporangium corresponds to a pinnule of the sorophore and is connected with the vein of the pinnule. The tissue adjacent to the sporangium forms a pocket-like indusium, recalling the indusium enclosing the sorus in Trichomanes, of the Hymenophyllaceae.

The gametophyte.—In Anemia, Mohria, and Lygodium the development of the gametophyte is much like that of the typical Leptosporangiatae. The growing point may be formed on one side of the apex, so that the thallus does not develop the characteristic heart shape; but in Lygodium the heart-shaped prothallium may be present, though often the two lobes are

of unequal size.

In the species of Schizaea that have been investigated, especially S. pusilla, the gametophyte is very different. It is a freely branched, filamentous structure, resembling an alga or the filamentous gametophyte of some species of Trichomanes. The species examined grow in wet situations, and this filamentous gametophyte may be an adaptation to such a habitat. It is well known that spores of many ferns grown in water, or under very wet conditions, tend to develop a filamentous form. Goebel and Bower

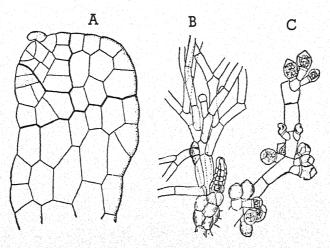


Fig. 222.—A, young gametophyte of Anemia Phyllitidis; B, female, C, male gametophyte of Schizaea pusilla (A, after Bauke; B, C, after Britton & Taylor).

are inclined to regard the filamentous gametophyte of *Schizaea* as a primitive rather than a secondary condition; but it seems to the writer that this is unlikely.

The antheridium resembles that of the Polypodiaceae; but the first wall, instead of being funnel-shaped, is nearly flat, so that the basal cell of the antheridium is a disc instead of a ring. In Lygodium the wall may be concave, approaching the funnel shape typical of the Polypodiaceae. In some cases the cap cell may undergo division. The number of spermatozoids in Lygodium circinnatum, according to Miss Twiss, may reach 156. In the other genera the number is less.

The archegonia are of the ordinary leptosporangiate type, but the neck is not so much curved. The development of the embryo has not been investigated. How far it differs from the typical leptosporangiate type and approaches the more generalized type of *Osmunda* remains to be discovered.

Relationships.—While there is much difference in the general morphology of the four genera, they are evidently all related and the family is a natural one. They all agree in the structure and development of the sporangium, which is always of marginal origin and has the very characteristic apical annulus. Bower concludes that their nearest living relations are the Osmundaceae but that they also show an approach to the typical Leptosporangiatae. Bower states: "Their undoubted antiquity and their close affinity on the one hand with the Simplices, and on the other with those Gradate Leptosporangiates that have marginal sori, are wholly in accord with that unusual combination of primitive and advanced features which is disclosed by the study of their living representatives."

A point of great interest is the evidence of relationship between the Schizaeaceae and the heterosporous Marsileaceae. This point will be discussed further when the Marsileaceae are considered.

HYMENOPHYLLACEAE

The large family Hymenophyllaceae with about five hundred species is cosmopolitan in its distribution, reaching its maximum development in the mountain rain-forests of the tropics and the wet lowland forests of the South Temperate Zone, e.g., the Westland forests of New Zealand, where there is an extraordinary profusion of these beautiful ferns. The growth conditions and distribution of the New Zealand Hymenophyllaceae have been very completely investigated by Professor J. E. Holloway. Some species form tufts of leaves growing on the floor of the forest and having a well-developed system of roots. Others may grow on rocks or stumps where sufficient moisture is available; but they are especially abundant as epiphytes, sometimes clothing the trunks of tree ferns or the trunks and

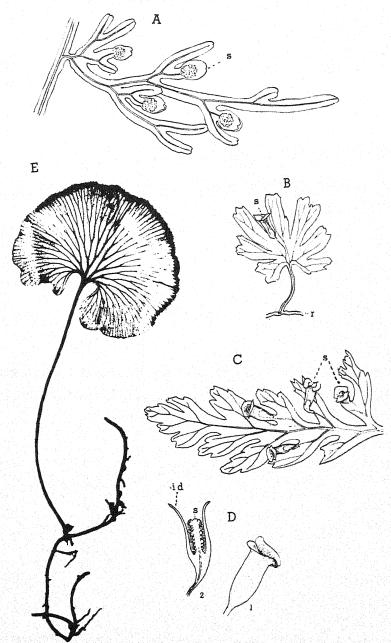


Fig. 223.—A, Hymenophyllum recurvum; s, sorus; B, Trichomanes parvulum; C, T. cyrtotheca; D, sorus of T. cyrtotheca; E, Trichomanes reniforme (E, photograph by Mr. John Poindexter).

branches of trees with a drapery of their delicate fronds. Few species occur in the North Temperate Zone. Two or three species of *Trichomanes* and one *Hymenophyllum* have been found in southern United States.

The most marked characteristic of nearly all species is the translucent membranaceous texture of the leaves. Except for the delicate veins, the lamina consists of a single layer of cells and they are popularly known as "filmy ferns." Some of the very small species which grow in close mats are readily mistaken for liverworts or mosses. This filmy structure is probably secondary and associated with the extremely humid conditions under which most of them grow. They might be compared with Leptopteris, a genus of the Osmundaceae where a somewhat similar condition is found.

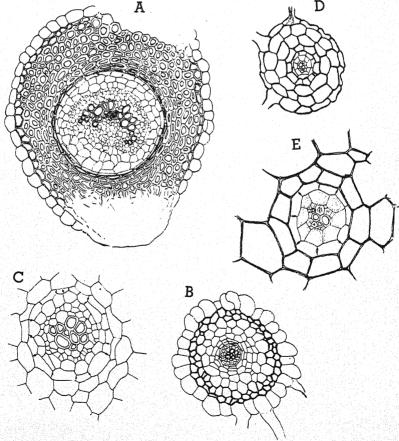


Fig. 224.—A, section of rhizome of Hymenophyllum recurvum; B, C, rhizome of Trichomanes venosum; D, section of root of Hymenophyllum recurvum; E, vascular bundle.

The Hymenophyllaceae include the smallest known ferns, some species, e.g., Trichomanes Motleyi, have leaves less than a centimeter in length. The largest are probably some species of Hymenophyllum. Holloway states that the pendent fronds of H. pulcherrinum may reach a length of two to three feet. Under favorable conditions the delicate lace-like fronds of the larger species are unsurpassed in beauty. Most of the species have slender rhizomes, which in the smallest species are not thicker than a thread. The leaves are placed in two rows on the dorsal side of the stem. In a few species of Trichomanes there is a short upright stem with spirally arranged leaves. In Hymenophyllum the rhizome is always dorsi-ventral.

The leaf.—While the leaf in most species is apparently pinnate, it seems to be rather a sympodial structure, "dichopodium," resulting from unequal dichotomy. This is generally evident in the terminal divisions of the frond apex. In some of the very small species the lamina is entire, with a single median vein. In some others it is flabellate with dichotomous venation, e.g., Trichomanes reniforme. In the compound leaves there is a vein extending into each leaf segment. In the fertile segments the sorus is borne on the margin, the vein being continued to form the receptacle of the sorus upon which the sporangia are developed. The young sorus is protected by a characteristic indusium. This is tubular in Trichomanes, while in Hymenophyllum it is composed of two lobes, like a bivalve shell. Hairs are found in many species, but the paleae (scales) found in most of the Polypodiaceae are absent.

Anatomy.—The structure of the rhizome, except for its much smaller size, is similar to that of the simpler Gleicheniaceae. The single axial vascular cylinder in Hymenophyllum is concentric. The phloem forms a continuous zone about the xylem, and there is a conspicuous pericycle. There is a good deal of variation found in Trichomanes. In some of the stouter species like T. radicans, there is a greater development of the xylem, and Boodle found two or three protoxylems. In some of the smaller species there is apparently a reduction of the phloem and the bundle assumes the collateral form. In the very small T. Motleyi, Karsten found that there was a complete absence of tracheary tissue except in the fertile frond. The cortex in the larger species is composed mainly of sclerenchyma; this is less developed in the more delicate species.

Axillary branches may be developed but often remain dormant. Bower suggests that these axillary buds may be the weaker branch of a dichotomy of the short apex and their apparently axillary position the result of the formation of a single leaf and the apex of the branch remaining undeveloped.

The apical growth of leaf and stem is from a single apical cell, as in the typical Leptosporangiatae. Usually the lamina of the leaf is composed of a single layer of uniform cells; in *Hymenophyllum dilatatum* and *Trichomanes reniforme*, however, there are three or four layers, but the mesophyll has no intercellular spaces and there are no stomata.

In a number of species of *Trichomanes* of the section *Hemiphlebium* some of the veins have no tracheary tissue and are sometimes known as pseudo-veins. These are presumably reduced from originally functional vascular bundles.

While the Hymenophyllaceae are as a rule markedly hygrophilous, some of them are adapted to survive a limited exposure to dry conditions. These species are of small size and are crowded together so as to check excessive evaporation. They may have no roots, and water is absorbed directly by the leaves, thus resembling liverworts and mosses exposed to similar conditions.

The root.—In the large terrestrial species of Trichomanes there is a well-developed root system which is of importance in the absorption of water and food. In the epiphytic species the roots play a secondary role and the absorption of water is mainly through the leaves. In many small species of Trichomanes roots are entirely absent, the slender rhizomes with their root hairs replacing the true roots.

The structure of the stele of the root varies more than in any other family of the Leptosporangiatae. According to Prantl all species of Hymenophyllum have diarch roots; the roots of Trichomanes pyxidiferum are monarch, like those of Ophioglossum moluccanum, while in T. brachypus there may be as many as nine xylem masses, a condition known elsewhere only in the Marattiaceae.

The sporangium.—The sporangia of the Hymenophyllaceae are developed from the margin of the sporophyll. The apex of a vein grows beyond the margin of the leaf and becomes the receptacle of the sorus upon which the sporangia are borne. The first sporangium arises from the apex of the receptacle. This in Hymenophyllum remains short and produces relatively few sporangia; but in Trichomanes a basal meristematic zone is formed from which new sporangia are developed in basipetal succession. This may continue for an indefinite period, and the receptacle, from which the older sporangia fall away, forms an elongated slender filament extending far beyond the tubular indusium recalling the columella of Anthoceros. This no doubt suggested the theory that there was a real homology between Anthoceros and the Hymenophyllaceae.

The tissues of the leaf surrounding the very young receptacle form a ring-shaped ridge which elongates and becomes the tubular indusium enclosing the sorus. In *Trichomanes* this becomes a trumpet-shaped envelope, in some species showing a two-lobed margin. In *Hymenophyllum* the indusium is completely divided into two similar valves.

The sporangium has a short stalk, and in general the early stages resemble those of *Gleichenia* or the Schizaeaceae. In *Trichomanes cyrtotheca* the tapetum is two-layered and, as in *Gleichenia*, the conspicuous annulus is oblique and is incomplete and interrupted on the ventral side of the sporangium where the dehiscence takes place. There is no definite stomium, and the opening is not vertical as in *Gleichenia* but is a somewhat oblique cleft, suggesting the transverse cleft of the Polypodiaceae.

The sporangia of Hymenophyllum are fewer in number but larger than those of Trichomanes, and the spore output is correspondingly greater. Bower states that in Hymenophyllum tunbridgense the spore number is 256 to 512, while in several species of Trichomanes the maximum number was 64.

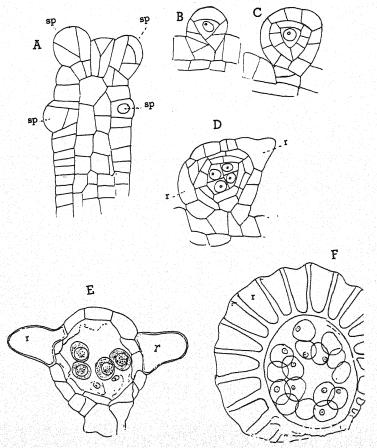


Fig. 225.—A, young sorus of Trichomanes cyrtotheca; sp. young sporangia; B-E, development of the sporangium; r, annulus; F, horizontal section of sporangium.

Gametophyte.—In some species of Trichomanes, e.g., T. pyxidijerum, the gametophyte is composed of extensively branched filaments, resembling the protonema of a moss or the filamentous prothallium of Schizaea. In other species, however, e.g., T. alatum, the prothallium becomes a flattened thallus much like that of the typical Leptosporangiatae.

In Hymenophyllum the prothallium is a ribbon-shaped thallus which branches either monopodially or dichotomously and is composed of a single layer of uniform cells. Branches may become detached and form new prothallia, or special gemmae may be produced in large numbers from the margins of the thallus and thus provide for a rapid vegetative increase of the gametophyte. It is not unusual to find extensive mats of the sterile prothallia which are easily mistaken for liverworts. Sometimes from the germinating gemmae small filamentous prothallia are developed bearing only antheridia. These prothallia much resemble those of Trichomanes.

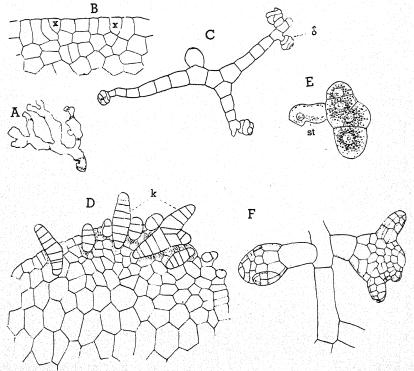


Fig. 226.—A, gametophyte of Hymenophyllum sp.; B, margin of gametophyte, showing initial cells, x; C, dwarf male gametophyte, developed from a gemma; D, margin of gametophyte of Hymenophyllum sp., showing gemmae, k; E, a single gemma; F, filamentous prothallium of $Trichomanes\ rigidum$, with archegoniophores (F, after Goebel).

Gametangia.—The antheridia in Hymenophyllum are mostly found on the margin of the thallose gametophyte or at the ends of the branches of the filamentous ones. They closely resemble the antheridia of Gleichenia in the arrangement of the parietal cells, which are more numerous than in the Polypodiaceae or Shizaeaceae. Instead of the two ring cells and the cap cell of the Polypodiaceae, the peripheral cells are more numerous and there are no complete ring cells, nor is there a definite cap cell.

The archegonia are formed near the growing points of the thallus margin. Before they are evident there is the formation of a small thickened region back of the growing point, so that a small archegonial cushion, like that in the typical ferns, is developed. In the filamentous gametophyte of *Trichomanes* the archegonial meristem is developed on a special lateral branch.

The development of the archegonium has not been studied in detail, but it probably does not differ essentially from that of *Gleichenia*, which it resembles in the straight or only slightly curved neck.

The embryo is still very imperfectly known, and further data as to its development are necessary before a comparison can be made with the embryology of other Leptosporangiatae.

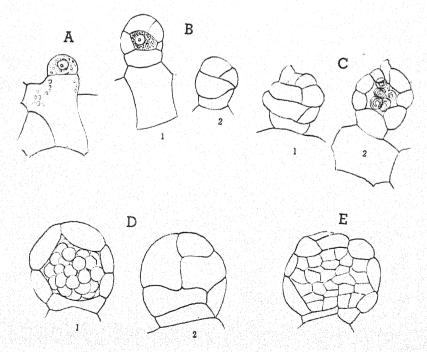


Fig. 227.—Development of the antheridium in Hymenophyllum sp.

Relationships.—The occurrence in the Carboniferous of sporangia which seem to resemble those of Hymenophyllaceae and have been named "Hymenophyllites" has been taken to indicate that the family can be traced back to the Palaeozoic era. This conclusion is not universally accepted, and the existence of Hymenophyllaceae at this remote period must for the present be considered as at least doubtful. There seems good reason to assume that their nearest living relations are the "Simplices"—Schizaeaceae and Gleicheniaceae—although it is not likely that they are derived directly from either of these families.

Bower believes that Trichomanes reniforme and Hymenophyllum dilatatum, in which the leaves are pluristratose, are probably the most primitive living representatives of the family. Holloway, who has made the most complete study of the family under natural conditions, concludes that the terrestrial, "tufted" species, like Trichomanes elongatus, which in habit are most like the typical ferns in stem structure and well-developed root system, may better represent the original types from which the more specialized types have developed.

From the primitive stock, whatever may have been its character, the two lines of development have diverged. Of the two, *Hymenophyllum*, in the character of both its gametophyte and its sporangium, has remained more uniform. In *Trichomanes* there has been a more marked specialization, shown in the extreme reduction of the tissues, especially the vascular bundles and the loss of roots, in some of the smaller species.

The development of the filmy leaf texture in both genera and the filamentous form of the prothallium in *Trichomanes* are associated with the extremely hygrophilous habit. Bower's conclusion is that the Hymenophyllaceae approach in both sporophyte and gametophyte the "protostelic" families of the Simplices, especially the Schizaeaceae. However, in both the antheridium and the sporangium they are more like *Gleichenia*.

As to the relative position of the two genera of the Hymenophyllaceae, Bower says (*The Ferns*, II, 250): "The more robust species with large spore output such as *T. reniforme* and *H. dilatatum* appear to occupy a central position phylogenetically. *Trichomanes* shows the greatest specialization and is on this account to be regarded as further removed from the original source."

LOXSOMACEAE

Loxsoma cunninghamii is an endemic fern from New Zealand. It was formerly placed in the Hymenophyllaceae, but as a result of more critical study it is now recognized as the type of a special family, Laxcomaceae. A second genus, Loxsomopsis, was later established to include three species from Central and South America. The leaves are upright and rigid and in

Loxsomopsis may be eight feet high. They are borne singly on a prostrate rhizome very much as in the Gleicheniaceae and Hymenophyllaceae.

The family seems to be a generalized one showing evidences of relationship on the one hand with the Hymenophyllaceae and on the other with the Dicksoniaceae, which includes a number of tree ferns. The sporangia are marginal and are borne on a receptacle at the apex of a vein very much as in *Trichomanes*, and like the latter are developed in basipetal succession. As in *Trichomanes* also the sorus is surrounded by a similar cup-shaped indusium. The sporangia themselves, however, especially in *Loxsomopsis*, are more like *Dicksonia* in both the form of the annulus and the dehiscence. The dermal appendages are hairs or bristles.

Goebel figures a prothallium of Loxsoma which closely resembles that of the typical Polypodiaceae, from which it differs in the presence of bristle-like appendages like those found in some of the tree ferns. The antheridia are said to be essentially like those of the Polypodiaceae.

Bower concludes: "In habit and anatomy they resemble the Dicksonia-Dennstaedtia series [of the Dicksoniaceae] while the sporangia of Loxsomopsis is very like that of Thyrsopteris or a short stalked type of Dicksonia. On the other hand there is a general similarity to the sorus and sporangia of the Hymenophyllaceae."

A Jurassic fossil, Stachypteris, has been suggested as not improbably related to the Loxsomaceae. The small number of living species and their widely separated habitats indicate that they are relicts of a once much more numerous and widespread group.

TREE FERNS: DICKSONIACEAE, CYATHEACEAE

The ferns reach their climax in the tree ferns, of which the most important genera are Dicksonia, Cyathea, and Alsophila. These magnificent ferns, like the Hymenophyllaceae, are best developed in the tropical mountain rain-forests and the wet forest lowlands of the South Temperate Zone. New Zealand, again, as in the case of the Hymenophyllaceae, shows a notably luxuriant growth of tree ferns. Cyathea medullaris and C. kermadecensis are unsurpassed by any other tree ferns; the latter may reach 70 feet in height, and C. medullaris is nearly as large. Some New Zealand tree ferns, e.g., Hemitelia Smithii, are found growing close to the great Franz Joseph glacier in the South Island, in about 42°, while it is also recorded from the subantartic Lord Auckland Islands about 50° south latitude. No tree ferns occur in the United States or Europe.

All of the tree ferns have been placed usually in a single family, Cyatheaceae; but Professor Bower in his recent studies on the ferns removes Dicksonia and its nearest allies from the Cyatheaceae and regards them as an entirely independent group, the Dicksoniaceae, more nearly related



Fig. 228.—Trunk of a tree fern, Absophila sp., showing leaf scars (photograph by Mr. John Poindexter).

to the "Marginales"—e.g., Hymenophyllaceae, Schizaeaceae, etc.—than to the Cyatheaceae, the sori of which are borne on the lower surface of the frond (i.e., they are Superficiales).

DICKSONIACEAE

Dicksonia, the type genus, includes about fifteen species of tree ferns characteristic of the South Temperate Zone, especially Australia, New Zealand, and adjacent islands. A single species from Central America is the only one in North America.

The best-known species, D. antarctica, from Australia, extends southward in Tasmania to 45°. A second monotypic genus, Thyrsopteris, is endemic in Juan Fernandez. The tree ferns of Hawaii are species of Cibotium. The latter and Dicksonia are large tree ferns with massive trunks covered with a thick mantle of roots and bearing a crown of gigantic fronds. The sori are marginal and enclosed in an indusium similar to that of the Hymenophyllaceae. In Thyrsopteris the indusium is cup-shaped, but in Cibotium it is composed of two valves much as in Hymenophyllum. The dermal appendages are hairs which sometimes form heavy felted masses about the young fronds.

Thyrsopteris elegans, the only species, differs from the other members of the family in having the sporangia borne

on special fertile pinnae, in which the lamina of the segments is almost completely suppressed, very much as in Osmunda. As in the Hymenophyllaceae, the sporangia are formed in basipetal succession upon the receptacle; but this process is of limited duration. The sporangium has a thick pedicel and a nearly vertical annulus, showing some resemblance to the Hymenophyllaceae and the Loxsomaceae. Bower thinks Thyrsopteris is the last

remnant of an archaic family—a possible relation to Coniopteris, a Jurassic fern.

Dicksonia and Cibotium, as might be expected from their large leaves, have a highly developed fibro-vascular system in the thick trunks. The vascular bundles form a dictyostele which in cross section shows the irregular form of the broad bundles of the dictyostele, forming an almost solid corrugated ring surrounding the thick central pith.

Bower has shown that the sorus in *Cibotium* is really marginal, developed from the end of a vein, as it is in the Hymenophyllaceae; but it becomes broader, the regular succession of the sporangia is much less evident, and there is an approach to the "mixed" condition found in the Polypodiaceae. In *Cibotium* the sporangia are long-stalked and the annulus almost vertical. There is a definite stomium, and the dehiscence is much like that in the Polypodiaceae.

The Dicksoniaceae, therefore, are to some degree intermediate between the less-specialized Marginales and some of the Polypodiaceae. Of the latter the subfamily Dennstaedtineae is included by Bower with the Dicksoniaceae. As in the latter, the dermal appendages are hairs, scales being quite absent. They are not tree ferns but have creeping stems bearing solitary, decompound, pinnate leaves. The sori are marginal with a two-

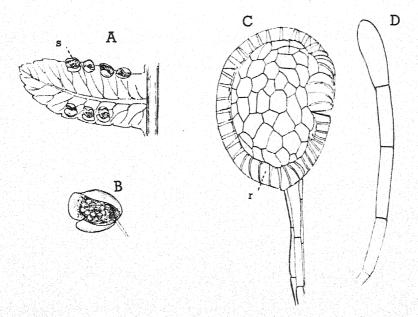


Fig. 229.—Cibotium Menziesii. A, pinnule with sori; B, single sorus; C, sporangium; r, annulus; D, paraphysis.

valved indusium. The sporangium in *Dennstaedtia* is that of the typical Polypodiaceae, having a three-rowed pedicel and vertical annulus. The sporangia, however, develop in regular basipetal succession as they do in Hymenophyllaceae. Of the fifteen species of *Dennstaedtia* one, *D. punctilobula*, is found in eastern United States. *Microlepia* has about ten species mainly tropical. Bower suggests that the Jurassic fossils, *Coniopteris*, may have been related to the existing Dicksoniaceae.

CYATHEACEAE

The Cyatheaceae, as recognized by Bower, includes only three large genera of tree ferns, Cyathea, Hemitelia, and Alsophila. These are cosmopolitan in their distribution, occurring in the moist tropics of both hemispheres, with some extratropical species, especially in the Australasian regions.

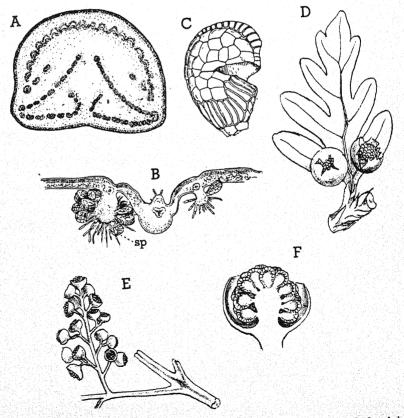


Fig. 230.—A, section of stipe of Absophila Cooperi; B, cross section of a leaflet of the same, with sporangia, sp; C, open sporangium; D, Cyathea microphylla; E. F, Thyrsopteris elegans (D, after Hooker; E, F, after Kuntze).

The sori are on the lower surface of the leaf, recalling the sori of Gleichenia, differing thus essentially from the marginal sori of the Dicksonia type.

The three genera include about four hundred species, mostly tree ferns, some of the species of Cyathea and Alsophila exceeding in size all other ferns. The stout upright trunk may occasionally fork, or sometimes lateral branches may develop. The trunk may be partially covered with a mat of adventitious roots, but often the surface of the trunk is mostly free of roots and is marked by conspicuous scars left by the fallen fronds. The leaves may reach gigantic dimensions—sometimes 5 to 6 meters in length, with the broad lamina usually bipinnate. Simply pinnate leaves are found in Alsophila phegopteroides and entire leaves in Cyathea sinuata. The venation and the position of the sori are much as in Gleichenia.

The structure of the stem in the Cyatheaceae is very complicated. The massive vascular bundles form a dictyostele probably resulting from a fusion of the leaf traces, which are composed of numerous separate strands like the Marattiales. The center of the stem is occupied by the pith, within which are numerous isolated vascular bundles, apparently of cauline origin like the commissural strands of the Marattiaceae; so that there is a certain similarity between the stem structures of the Cyatheaceae and the Marattiaceae.

The young leaves and stem apex are covered with broad "paleae," like the scales so characteristic of the Polypodiaceae. In this particular, also, the Cyatheaceae differ from the Dicksoniaceae where the dermal appendages are hairs.

The sporangium.—The sori, like those of Gleichenia, form a single series on either side of the midrib of the pinnule. In Alsophila the sori are naked, as they are in Gleichenia; but in Hemitelia there is an imperfect indusium consisting of a basal scale varying much in degree of development. In Cyathea the sorus is enclosed in a globular indusium almost entirely closed when young but becoming cup-shaped with later growth of the sorus.

The sporangia are borne on a conical receptacle. The first sporangium is terminal; the later ones are developed in basipetal succession, but their number is limited. The early divisions in the sporangium differ from those in the Dicksoniaceae and most other Leptosporangiatae. The terminal cell of the young sporangium has the form of a biconvex lens, "a two-sided" apical cell, instead of the tetrahedral form characteristic of the typical Leptosporangiatae. There are therefore two series of segments instead of three; and the short stalk of the sporangium, as the result of a radial division in the segments, has four rows instead of the three in the Dicksoniaceae and the Polypodiaceae. Bower states that this type of apical cell is

found also in *Dipteris* and *Metaxya*. The ripe sporangium has a nearly complete, slightly oblique annulus.

Gametophyte.—The gametophyte is much like that of the Polypodiaceae, but the antheridia show a somewhat intermediate condition between the Polypodiaceae and Gleicheniaceae. There are two extra parietal cells, as compared with the Polypodiaceae, and a division of the cap cell forming a definite operculum.

The first divisions of the embryo are like those of the Polypodiaceae, but the further history of the embryo has not been followed.

Two monotypic ferns from the American tropics, Lophosoria quadripinnata and Metaxya rostrata, sometimes included in the genus Alsophila, show certain characters indicating a possible relationship also with Gleichenia. Bower has proposed a special family, Protocyatheaceae, to include these intermediate between Gleicheniaceae and Cyatheaceae.

Relationships.—Alsophila, as regards the sporangium, is probably the most primitive of the Cyatheaceae. The sori, as in Gleichenia, have no indusium; and the sporangium resembles that of Gleichenia in form and in the oblique annulus. However, the sporangia are of the "gradate" type and the dehiscence is transverse, thus resembling the Polypodiaceae.

Hemitelia shows an advance in the development of an indusium, which in Cyathea becomes the characteristic cup-shaped structure. How far the "Protocyatheaceae" really connect the Gleicheniaceae and the Cyatheaceae is somewhat problematical but there is undoubtedly some reason for such a conclusion.

While on the one hand the Cyatheaceae show evidences of relationship with the Gleicheniaceae, there are also suggestions of the gradate Hymenophyllaceae. There is also strong evidence of relationship with the dominant Leptosporangiatae, viz., the Polypodiaceae. These are mostly "Mixtae," i.e., have sporangia of different ages in the sorus.

POLYPODIACEAE, THE MODERN FERNS

The great majority of the living ferns are referred usually to a single family, Polypodiaceae; but there is increasing evidence to show that the family, as generally recognized, includes several independent phyla. Professor Bower, in his extended study of these forms, gives convincing reasons for this conclusion. He believes that certain genera are derived from the Marginales through the Dicksoniaceae; that others show evidences of possible relationships with the Osmundaceae; and that still others are derived from Superficiales like the Cyatheaceae and Dipteridaceae. If Professor Bower's conclusions are accepted, it is clear that the Polypodiaceae can no longer be maintained as a natural family. Nevertheless the genera included in the Polypodiaceae are sufficiently alike in the characters of

both their vegetative and their reproductive parts to make it unnecessary to treat in detail the different divisions recognized by Bower, especially as these structures have been already discussed at some length in the preceding chapter.

The Polypodiaceae constitute emphatically the modern fern-type. Outnumbering several times all the other families, they are by far the most widespread and adaptable of the existing pteridophytes. That they are essentially a modern type is also indicated by the fossil record, which, however, is far from complete. While there are some doubtful records in the Mesozoic, it is only in the Tertiary that they can be definitely identified. Some existing genera, e.g., Onoclea and Acrostichum, occur in the Eocene, and in the later Tertiary they become more abundant.

Many genera are cosmopolitan, and some species have a very wide distribution. Thus the common bracken (*Pteridium aquilinum*) is found in nearly every part of the world. As a rule the ferns are not aggressive; but occasionally, as in the case of the bracken, they may become trouble-some weeds.

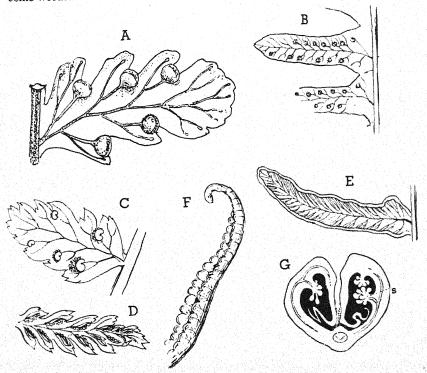


Fig. 231.—Polypodiaceae. A, Dennstaedtia; B, Polypodium; C, Aspidium; D, Asplenium; E, Pteridium; F. G. Onoclea Struthiopteris.

For the most part the Polypodiaceae, like the other ferns, are best developed in regions of abundant moisture and moderate temperature, like New Zealand and many oceanic islands, where they form a conspicuous feature of the vegetation. In the mountain rain-forests of the tropics and the South Temperate Zone there are many epiphytes, and even in the Northern Hemisphere there are regions, like the northwest Pacific Coast, where a few species of ferns, e.g., *Polypodium glycorrhiza*, sometimes grow on the trunks or branches of trees.

Many tropical epiphytic ferns, like Asplenium nidus, accumulate humus between the persistent leaf bases, this store of humus being doubtless of importance in the growth of the plant. In species of Polypodium and Platycerium there are special modified leaves which have the same function.

In regions of periodic drought the epiphytic ferns, like the liverworts

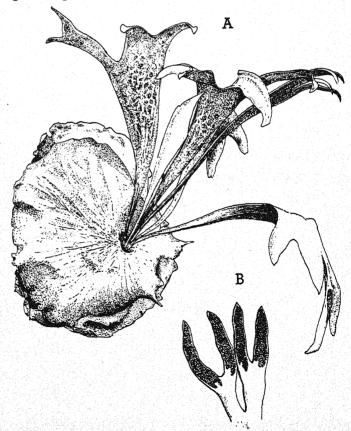


Fig. 232.—Platycerium alcicorne. A, plant showing the single basal sterile leaves and the forked sporophylls; B, tip of fertile region of sporophyll, showing the crowded sporangia (A, after Coulter; B, after Diels).

and mosses, can become dried up during the dry season, reviving quickly when moistened. The same is true of many ferns growing in rocks or on the ground. Species of *Pellaea* are in this category, and in coastal California the leaves of the "goldback fern" (*Gymnogramme triangularis*) may be completely dried but will quickly absorb water and resume their activity.

Very few ferns are true aquatics. A notable exception is the tropical Ceratopteris thalictroides, which is a genuine water plant; and the hand-

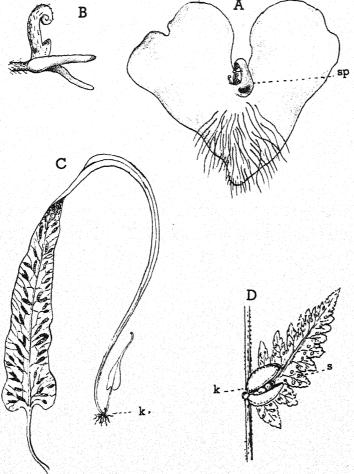


Fig. 233.—Vegetative reproduction in Leptosporangiates. A, prothallium of Pteris cretica, with apogamous young sporophyte, sp; B, bud developed from root apex of Asplenium esculentum; C, Camptosorus rhizophyllus, with bud at leaf apex; D, Cystopteris bulbifera; k, bud at base of leaflet (A, after De Bary; B, after Rostowzew).

some fern, Acrostichum aureum, is a conspicuous feature of the tropical mangrove swamps.

Both radial and dorsi-ventral stems are found in the Polypodiaceae, but in no cases do they reach the dimensions of a real tree fern. The prostrate, dorsi-ventral stem may reach a considerable length and branch freely, as it does in the common bracken.

The leaf.—The leaves, while never equaling in size those of some of the Marattiaceae and Cyatheaceae, may attain a length of 2 to 3 meters, or in some of the epiphytic species of Polypodium may hardly exceed a centimeter in length. They may be entire, e.g., in Asplenium Nidus, Scolopendrium, and Vittaria, but usually are compound and pinnately divided. Less commonly the frond is dichotomous, e.g., in Platycerium and Adiantum. In the pinnate leaves the pinnae (or pinnules) have, as a rule, a distinct midrib with free lateral dichotomous veins. There are, however, many cases of reticulate venation suggesting Ophioglossum—e.g., Woodwardia, Onoclea, and Vittaria. Less frequently, e.g., in Adiantum, the venation is strictly dichotomous and no midrib is present.

The dermal appendages are either hairs or scales, which may have a terminal glandular cell. The scales or paleae, as in the Cyatheaceae, are especially developed on the stem apex and young leaves, where they probably are efficient in retaining moisture.

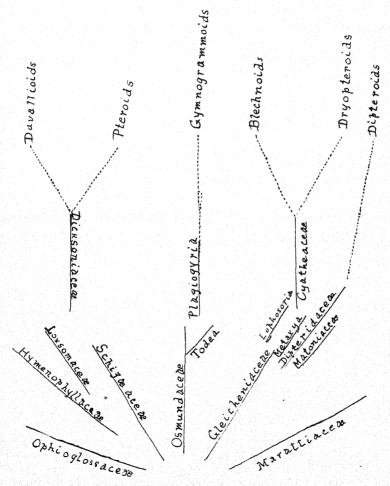
The roots.—The roots in the Polypodiaceae are numerous but do not show any definite relation in number to the leaves. They are typically diarch and the secondary roots arise in regular succession—in two series corresponding to the two protoxylems of the xylem plate. The secondary roots branch in a similar manner. The formation of buds from the roots has been observed in some cases. Thus in Asplenium esculentum Rostowzew shows a leafy shoot developed from the apex of a root.

Sporangium.—The sporangia of the Polypodiaceae are very uniform in structure. The slender pedicel is composed of three rows of cells. The vertical annulus extends over the apex of the capsule as far as the conspicuous transverse stomium, marking the point where the cleft appears at dehiscence. There are typically 16 spore mother cells and 64 spores, although there are sometimes a smaller number.

The shape and position of the sori differ greatly and form the principle criterion in classification.

Bower has pointed out that in the Polypodiaceae the position of the sorus in some genera indicates that they have been derived from ancestors in which the sorus is marginal, e.g., Dicksoniaceae. Others have the sori of the superficial type and suggest a deviation from forms like the Cyatheaceae. Such differences among the Polypodiaceae support Bower's conclusion that the Polypodiaceae should no longer be accepted as a single

family but should be divided into several co-ordinate groups (families?). Bower divides the Polypodiaceae into eleven groups, viz., Hypolepis; Davallioids; Pteroids; Gymnogrammoids; Dryopteroids; Asplenoids; Onocleoids; Blechnoids; Dipteroids; Metaxyoids; Vittarioids. There are also a number of genera which cannot be assigned definitely to any of the above. For a detailed account of the relationships of these groups of the Polypodiaceae the reader may be referred to Volume III of Professor Bower's treatise on the ferns.



Botry opteridace ae

Fig. 234.—Diagram showing phylogeny of the Filicineae (after Bower).

CHAPTER XVII

THE HETEROSPOROUS LEPTOSPORANGIATAE

Two leptosporangiate families, Salviniaceae and Marsileaceae, show marked heterospory and are generally put into a special order Hydropterides, or Rhizocarpeae. Except that they are heterosporous, they show very little evidence of near relationship; and it is evident that heterospory has developed independently in the two families, which have come from quite different homosporous ancestors.

SALVINIACEAE

The Salviniaceae are floating aquatics thus differing in habit from any other pteridophytes. The sporangia, however, are of the typical leptosporangiate structure, and the family is undoubtedly derived from some homosporous leptosporangiate ancestors; but it is by no means certain to which one of the homosporous families they are most nearly related. The family includes two genera, Salvinia and Azolla.

Salvinia includes about a dozen species, mostly tropical; but a single one, S. natans, is found in Europe and in a few places in the United States. Of the four or five species of Azolla two, A. caroliniana and A. filiculoides, are found, respectively, in the Atlantic and Pacific areas of the United States, extending into South America.

In both genera the plant branches freely, the branches readily becoming free; and the plants thus multiply rapidly and may cover considerable areas of the water surface almost to the exclusion of other vegetation. The simple leaves of Azolla form two dorsal rows; in Salvinia there are also two rows of ventral leaves. The latter are composed of a cluster of slender root-like filaments, covered with superficial hairs—and evidently serving the purpose of roots, the latter being absent. In Azolla there are no ventral leaves, but true roots are developed from the ventral surface of the stem.

The sporangia in Salvinia are borne in a globular "sporocarp," which consists of a central placenta or columella much as in the Hymenophyllaceae, while the wall of the sporocarp is comparable to the tubular indusium of Trichomanes or that of the Cyatheaceae. In Azolla the microsporangial sporocarp is also globular, but the megasporial sporocarp is much smaller and closely appressed to the solitary megasporangium.

The stem in both Salvinia and Azolla grows from a two-sided apical cell, and each segment cut off from it divides into a dorsal and a ventral

cell so that a transverse section back of the apex shows a regular quadrant division. In Azolla the leaves develop from the dorsal region, while the branches and roots are ventral. In Salvinia, where there are no roots, they are replaced by the ventral submersed leaves.

In Azolla the first division in the mother cell of a leaf divides it vertically into equal parts, and there is no trace of an apical cell. In Salvinia, however, the young leaf shows a definite apical growth, like that of most typical ferns. The early divisions in the young leaf of Azolla are not unlike those in some of the Hymenophyllaceae. The mature stem in the Salvinia-

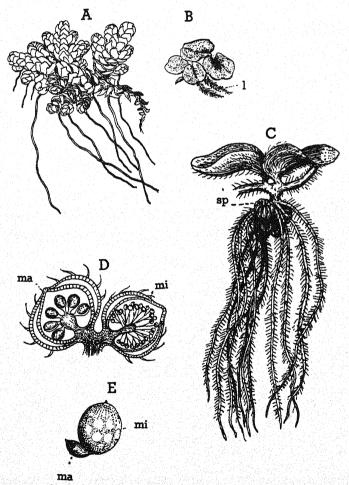


Fig. 235.—Salviniaceae. A, Azolla filiculoides; B, Salvinia natans; l, submersed leaf lobes; C, Salvinia natans; sp, sporocarps; D, sections of sporocarps of Salvinia; ma, megasporangia; mi, microsporangia; E, sporocarps of Azolla filiculoides (C, D, after Luerssen).

ceae has a single axial bundle, concentric in structure and with a definite endodermis.

In Azolla true roots are present but are much less numerous than the leaves. They arise from superficial cells but are surrounded by a sheath formed by the primary root cap which is continuous with the epidermis of the young root. A lacuna forms between this sheath and the root enclosed within it.

The leaves in Azolla are divided into a dorsal and a ventral lobe. The latter is submersed and in the fertile leaves bears the sporocarps. In the sterile leaves the ventral lobe consists of a single layer of cells, except in the middle, where there is a simple vein surrounded by a small amount of mesophyll. The dorsal lobe has a large cavity near its base which always harbors a colony of a peculiar blue-green alga, Anabaena Azollae. There is a definite epidermis with stomata and well-developed mesophyll composed of elongated cells. The vascular bundle is rudimentary.

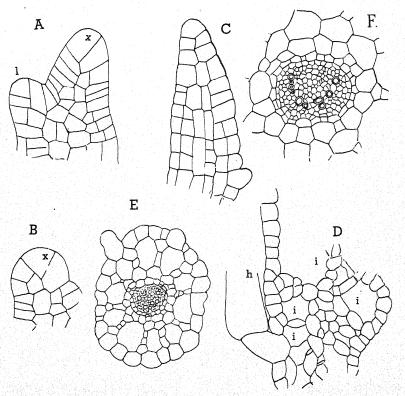


Fig. 236.—A, horizontal section of stem apex of Salvinia natans; l, young leaf; B, young leaf showing apical cell; C, section of a segment of a ventral leaf; D, section of a dorsal leaf; i, lacunae; h, hair; E, cross section of stem; F, vascular bundle of stem.

In Salvinia the thick, oval, dorsal leaves are traversed by a single vascular bundle. A section of the leaf shows an upper and lower epidermis, but no stomata are present. The mesophyll consists of two tiers of large lacunae separated by single layers of cells. The ventral leaves at an early stage divide into several segments, each having a definite apical growth and becoming greatly elongated, simulating roots. The leaves of Salvinia are in whorls of three, two dorsal and one ventral, which alternate, so that there are six rows altogether.

Sporangia.—The two sporocarps in Azolla filiculoides are formed from an equal division of the ventral lobe of the fertile leaf and each half of the lobe becomes at once the mother cell of a sporocarp. In Salvinia the sporocarps are formed at the base of some of the segments of the ventral leaves. In the young sporocarp there is soon developed a tetrahedral apical cell from whose regular division and growth the young sorus or receptacle is developed. The sporangia are formed from this receptacle very much as in the Hymenophyllaceae, and there is soon formed about the receptacle an indusium which encloses the sorus and may be compared with that of Trichomanes. This indusium finally forms the wall of the globular sporocarp. The wall of the sporocarp is composed of two layers. In Salvinia there are longitudinal lacunae between the two layers, so that the exterior of the sporocarp shows regular longitudinal ridges.

The megasporangia and microsporangia are borne in separate sporocarps, which in *Salvinia* are similar in size but in *Azolla* are of unequal size, only a single megasporangium being developed in the sporocarp, which is much smaller than that containing the microsporangia.

In Salvinia the two sorts of sporocarp are much alike. There are several megasporangia, although the number is much less than the microsporangia. In Azolla the solitary megasporangium is formed directly from the apex of the receptacle. Sometimes abortive microsporangia can be seen below the megasporangium. The indusium remains permanently closely appressed to the megasporangium; and the young megasporangium, closely invested with the indusium, recalls a young ovule with a single integument. In the microsporangial sorus of Azolla the apex of the columella is apparently an abortive megasporangium.

The early development of the sporangia does not differ from that of the typical Leptosporangiatae, up to the last division of the archesporium. In the microsporangium there are sixteen spore mother cells, and in the megasporangium eight. All of the mother cells undergo the tetrad division, resulting in 32 young megaspores and 64 microspores. All of the latter normally develop; but of the megaspores only a single one matures, the others, together with the disintegrated tapetum, serving to nourish the solitary functional megaspore, which when ripe completely fills the spo-

rangium. The outer wall of the megaspore becomes greatly thickened and in Azolla has excrescences evidently deposited by the nucleated protoplasm which surrounds the developing spore. These "episporic" structures in Azolla include three large masses above the apex of the megaspore. In the microsporangium the spores are embedded in a mass of foamy episporic material, which later separates into several "massulae." To the surface of the massulae are attached the anchor-like glochidia. These glochidia are not found in A. pinnata and A. nilotica.

During the growth of the megasporangium filaments of Anabaena enter the opening of the indusium and remain dormant until the germination of the megaspore, when they infect the young sporophyte while it is still attached to the megaspore.

The megasporangia are nearly sessile, but the microsporangia have long slender pedicels which in *Azolla filiculoides* are composed of two, sometimes three, rows of cells. No annulus can be recognized. In *Salvinia* the microsporangium may sometimes be borne upon the slender branches of a forked sporangiophore, and there is no division into massulae of the episporic matrix in which the spores are embedded.

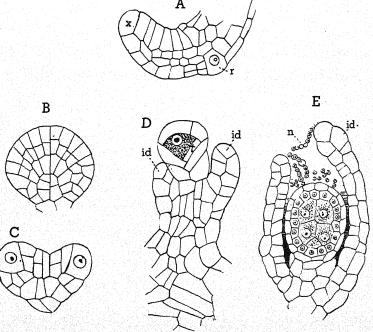


Fig. 237.—A, stem apex of Azolla filiculoides; r, young root; B, lobe of a young sterile leaf; C, fertile leaf segment with two young sporocarps; D, young megasporangium; id, indusium; E, an older megasporangium; n, Anabaena filaments.

The gametophyte.—The massulae enclosing the microspores in Azolla are set free from the sporangium and often attach themselves to the filaments developed from the outer surface of the megaspores. In Salvinia, where the episporic matrix is not divided into massulae, it remains within the sporangium wall. The microspores germinate while still enclosed in the episporic matrix, but are near the surface, and the gametophyte can reach the surrounding water and discharge the spermatozoids. In Salvinia the gametophyte penetrates also the sporangium wall.

The germinating microspore in Azolla increases in size and ruptures the spore wall. The cell elongates and divides into a basal and a terminal cell, the latter increasing in size and pushing through the surface of the massula. From the large basal cell a small prothallial cell is cut off, while the terminal cell becomes the antheridium. After a series of divisions eight spermatocytes are formed, enclosed by five parietal cells. The male gametophyte in Salvinia is larger and more elongated than that in Azolla, and the spermatocytes are in two groups, perhaps representing two antheridia. This interpretation has also been applied to Azolla. The spermatozoids are multiciliate and much like those of the typical ferns.

In Azolla, before the megaspore germinates the sporangium wall is broken down and the rough epispore, from which extend many fine filaments, is exposed. The glochidia of the microsporic massulae become at-

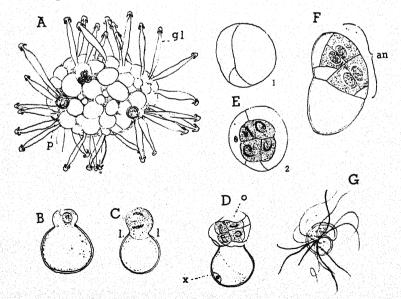


Fig. 238.—A, massula of Azolla filiculoides, with enclosed microspores; gl., glochidia; B-E, development of male gametophyte; E, cross section; F, male gametophyte of Salvinia; an, antheridium; G, spermatozoid of Salvinia.

tached to the filaments, thus bringing the male and female gametophytes near each other.

The first division in the megaspore in Azolla cuts off a small lenticular cell from the upper portion of the spore. This is the mother cell of the prothallium, while the much larger lower cell is filled with food materials serving to nourish the gametophyte and young embryo sporophyte. The prothallial cell undergoes a series of divisions, resulting in a central archegonium. There is now a rapid growth in the prothallium, which breaks through the spore membrane, exposes the archegonium, and soon develops chlorophyll. At this time the prothallium is nearly hemispherical. If the first archegonium is fertilized, no others are developed; but if it is abortive, several secondary ones may be formed. The growth, however, is limited, as there is relatively little chlorophyll, and is mainly at the expense of the stored food in the spore.

The lower nucleus resulting from the first division in the spore undergoes repeated division, but no cell walls are formed. The development of the female gametophyte in *Salvinia* is similar to that in *Azolla*, but it is much larger and there is in it a greater amount of green tissue and a corresponding increase in the number of archegonia. The early stages of the archegonium are much like those of the homosporous ferns, but the neck is shorter and the neck canal cell may remain undivided.

The embryo.—In the early divisions of the embryo Azolla filiculoides

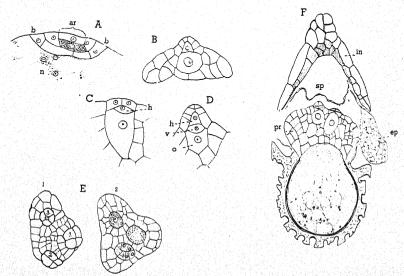


Fig. 239.—A, B, young female gametophytes of Azolla; C, D, young archegonia; h, neck; v, ventral canal cell; E, transverse sections of an older prothallium; F, section of megaspore of Azolla filiculoides with full-grown prothallium, pr; in, indusium; ep, per nium.

resembles the Polypodiaceae, except that the basal wall is usually transverse to the axis of the archegonium. There is a regular quadrant division, the stem and cotyledon being formed from the epibasal quadrants, the foot and root from the hypobasal region. The first division in the stem quadrant establishes the two-sided apical cell typical of the adult sporophyte. The first division in the cotyledon quadrant is median, an indication of the two lobes of the older leaves. The cotyledon becomes a funnel-shaped sheath, enclosing the stem apex. The primary root is formed in the same way as that of the Polypodiaceae. The foot is conspicuous and becomes elongated below the base of the root. The second leaf is developed from the first segment of the apical cell of the stem and each successive segment forms a new leaf. The vascular bundles are not evident until the second leaf is well advanced. The bundles from the cotyledon and the second leaf unite in the center of the sporophyte, where they are joined by the stele of the root. Apparently there is no cauline stele.

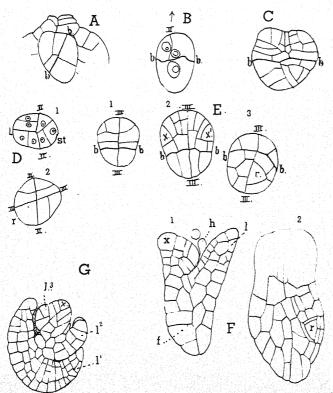


Fig. 240.—Development of the embryo in Azolla filiculoides; D, G, horizontal sections; E, transverse, the others median longitudinal; b, basal wall; l, leaves; r, root.

The development of the embryo in Salvinia is much like that of Azolla. The most marked difference is the absence of a root. Yasui states, however, that the rudiment of a root can be demonstrated in the very young embryo but that it very soon becomes merged with the foot and is no longer recognizable.

Relationships.—There are some reasons for assuming that of the homosporous leptosporangiates the Hymenophyllaceae are, on the whole, most nearly related to the Salviniaceae. The Hymenophyllaceae are characteristically hygrophilous in habit, although none of them are actually aquatics. The derivation of the Salviniaceae from forms related to the Hymenophyllaceae is, at any rate, conceivable.

The simple leaves of the Salviniaceae might be compared with some of the less-specialized Hymenophyllaceae like *Trichomanes reniforme* or *T. muscites*. The latter, as well as some other species, is rootless, like *Salvinia*. There are, however, marked differences in the leaf structure between the two families. The filmy leaves of the typical Hymenophyllaceae, except for the veins, consist of a single layer of cells. In the Salviniaceae the leaves have a definite epidermis and mesophyll. It may be recalled, however, that in *Trichomanes reniforme*, which has been considered to be a more primitive type, the leaves have several layers of cells, while in *Azolla* the ventral lobe of the leaf is composed of a single layer.

Of the two genera of the Salviniaceae, Salvinia, on the whole, is probably the less specialized. Its leaves have a definite apical growth, while in Azolla the growth is marginal. In this respect Azolla more nearly resembles some of the Hymenophyllaceae. The peculiar adaptation of the leaf of Azolla for its association with the symbiotic Anabaena is probably a secondary condition not found in Salvinia.

The sporocarp of the Salviniaceae can be readily homologized with the sorus of the Hymenophyllaceae, especially *Trichomanes*, where the marginal sorus terminates a vein and is enclosed in a cup-shaped or tubular indusium. This is especially evident in *Azolla*, where the first sporangium is terminal on the receptacle and the later ones are developed basipetally. Heterospory is farther advanced in *Azolla* than in *Salvinia*; in the latter the two sorts of sporocarps are much more alike, while in *Azolla* only a single megasporangium matures and the sporocarp is very much smaller than that containing the microsporangia.

The female gametophyte in Salvinia is less reduced than in Azolla, thus approaching more nearly the condition in the homosporous ferns; and together with the less-marked heterospory this condition indicates that Salvinia is more nearly related to the homosporous ferns from which the family has been derived.

While these conclusions must be taken with reservations, the evidence

at hand seems to indicate that the ancestors of the Salviniaceae were leptosporangiate ferns, of which the Hymenophyllaceae are the nearest living representatives. Of the Hymenophyllaceae, *Trichomanes* most nearly approaches the Salviniaceae. This is seen in the development of the young leaves and the structure of the sorus and indusium. The absence of roots in some species of *Trichomanes* may be cited, and the filamentous prothallium of some species may be associated with a semiaquatic condition, which may have finally led to the forms with the aquatic habit of the Salviniaceae.

MARSILEACEAE

The Marsileaceae differ much less from the homosporous Leptosporangiatae than do the Salviniaceae. They have structurally much in common with the Schizaeaceae to which they are perhaps directly related.

Of the three genera included in the family, two, Marsilea and Pilularia, have a wide distribution in both the Eastern and Western hemispheres. The third genus, Regnellidium, is known as yet only from Brazil.

The Marsileaceae are aquatic—or more accurately amphibious—plants with slender rhizomes attached to the substratum by well-developed roots.

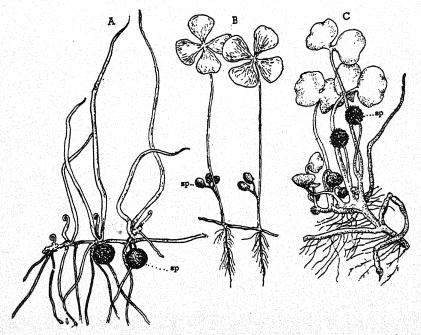


Fig. 241.—Marsileaceae. A, Pilularia Americana; B, Marsilea quadrifolia; C, Regnellidium diphyllum; sp, sporocarps (B, after Lucrssen; C, from Eames, after Meunier).

The young plants are more or less completely submersed, but most species of *Marsilea* usually grow in temporary ponds which dry up before the sporocarps are mature, and the latter complete their growth after the plants are completely exposed to the air. There are over fifty species of *Marsilea*, widely distributed through the warmer parts of the world. The six species of *Pilularia* occur in such widely separate countries as Europe, California, Bolivia, New Zealand, and Australia. *Pilularia* is the simplest and probably the most primitive member of the family. *P. globulifera*, the best-known species, occurs in many parts of Europe. *P. americana* is found in California and also in some other parts of western United States. It is a very inconspicuous plant and probably much commoner than is generally supposed.

The slender creeping rhizome has the delicate filiform leaves which are only 2 to 4 centimeters long, separated by elongated internodes. The young leaves are coiled (circinate) like those of the typical ferns. At the base of the leaf a bud is formed which develops a branch structurally like the main axis. Roots are also formed at each node. Bower concludes that the nodal buds are the result of repeated unequal dichotomy of the apex of the main axis. The development of the plant body in *Marsilea* is essentially like that in *Pilularia*, but there are four wedge-shaped leaflets, making the leaf look like a four-leaved clover. Where the plant is submersed, the elongated petioles cause the leaflets to float on the surface of the water. *Regnellidium* has a bifid leaf lamina borne on long petioles.

The sporangia are contained in sporocarps, stalked bodies attached either near the base of the petiole or some distance higher up. There is generally a single one; but in *M. quadrifolia* there may be two or three at

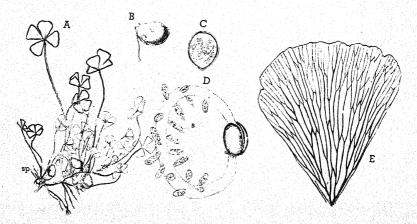


Fig. 242.—A, Marsilea vestita; sp, sporocarps; B, C, sporocarps of the same; D, germinating sporocarp; s, sori; E, leaflet showing venation.

the ends of branches from a common pedicel. In *M. polycarpa* there is a much larger number of single sporocarps forming a series. The sporocarps may be considered as greatly modified leaf segments or pinnae. It has been shown that they are lateral structures and may, perhaps, be best compared to the fertile pinnae of *Anemia* of the Schizaeaceae. Within the sporocarp are the sori, producing both micro- and megasporangia.

The growth of the stem is from a tetrahedral apical cell like that of most ferns. The young leaf also has a definite apical cell. In *Marsilea* the very young leaf grows from a two-sided apical cell. A lateral lobe is formed on each side of the young lamina so that it appears three-lobed. The terminal lobe then divides vertically and the four-lobed form of the leaf lamina is completed.

There is a central stele, which in longitudinal sections of the young stem apex seems to be continued beyond the youngest leaves and may perhaps be a true cauline structure. When complete it is a siphonostele with outer and inner endodermis. In the terrestrial plant the central pith is composed of sclerenchyma. In *Pilularia* there is no inner endodermis; and

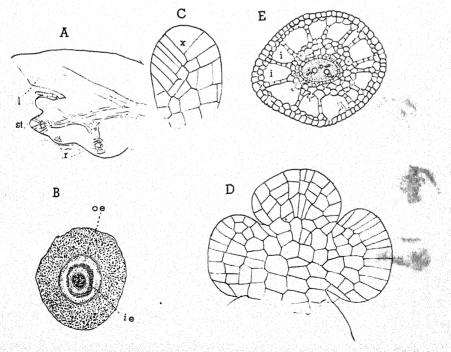


Fig. 243.—A, stem apex of Marsilea vestita; st, the growing point; l, leaf; r, young root; B, cross section of mature stem, the vascular bundle has outer and inner endodermis; C, young leaf, with apical cell; D, an older leaf; E, section of the petiole.

according to Johnson the pith is nearly or quite absent, the vascular cylinder thus approaching the condition of a simple concentric bundle or protostele. The structure of the stem bundle in *Marsilea vestita* closely resembles that of *Anemia hirsuta*.

The leaf.—The petiole of the leaf in Marsilea has a single concentric vascular bundle. The venation of the leaflets is dichotomous but includes some anastomosing of the veins. In Anemia the venation is commonly an open dichotomy; but in some species, e.g., A. Phyllitidis, there are anastomoses as in Marsilea. In Regnellidium there is open dichotomous venation. The structure of the roots is essentially the same as in the typical ferns.

The sporocarp.—The simplest form of sporocarp is that of Pilularia. It is a globular body borne on a short pedicel attached to the base of the leaf. It originates as a lateral outgrowth of the very young leaf. It soon assumes a nearly globular form, and at the apex four small prominences appear, which may be interpreted as leaflets. Johnson has shown that these are lateral organs and that the sporocarp is dorsi-ventral, i.e., is bilaterally symmetrical.

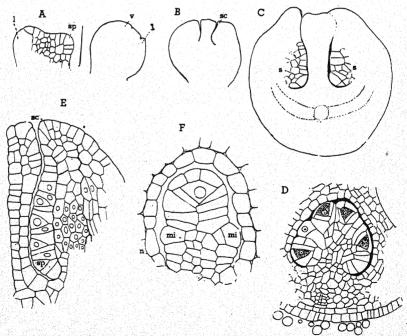


Fig. 244.—A, very young sporophyll of *Pilularia Americana*; sp., young sporocarp; B, somewhat older stages; v, apex of sporocarp; l, secondary lobe; sc, sorus canal; C, an older sporocarp; s, sori; D, an older sorus, showing sporangia; E, section of a young sporocarp of *Marsilea quadrifolia*; sp, young sporangia; sc, sorus-canal; F, section of sorus (E, F, after Johnson).

Only the extreme tips of the "leaves" are free; otherwise they are completely fused togther and form a solid globular body. A little later a small pit is formed at the base of each leaflet. These pits are separated by the coherent margins of the leaflets, and as the young sporocarp grows these pits become deep cavities, the "sorus canals," which are separated from each other by the tissue representing the coherent margins of the leaflets. The axial region of the sporophyte is occupied by a sort of columella. The four cavities rapidly increase in size with the growth of the sporocarp; but the sorus which forms an elongated cushion occupying the middle of the lobe almost completely fills the space between the lobe and the columella. Johnson states that the sorus arises from a single marginal cell in each of the four segments. The first sporangia are formed at the base of the sorus and their development is toward the apex; later secondary sporangia may be formed. Those in the lower part of the sorus, i.e., the oldest ones, develop into megasporangia, the upper ones into microsporangia.

Except for the number and position of the sori and the relative positions of the two sorts of sporangia, Marsilea agrees with Pilularia. The sorus canals form two longitudinal rows along the sides of the elongated young sporocarp, which is evidently a dorsi-ventral body which may be compared to the pinnate sorophore of Schizaea pusilla. Occupying the middle line of each sorus is a row of large tetrahedral cells from which three sets of lateral segments are cut off. From the tetrahedral apical cells the megasporangia are formed, while from the early segments the microsporangia are developed. A comparison of the very young sorophore of Schizaea, according to Prantl, shows that when the marginal sporangia are first recognizable the lamina of the pinnule is almost entirely suppressed and the resemblance to a similar stage in the sporocarp of Marsilea is very striking. In both cases the origin of the sporangia from marginal cells is significant.

The development of the sporangium in the Marsileaceae is typically of the leptosporangiate type and is very much like that of the Schizaeaceae. The apical growth in the sporangium is checked earlier in the first-formed ones, which have a very short pedicel. The secondary ones, which are always microsporangia, have longer pedicels. The tapetum has regularly two layers of cells. There are in *Pilularia* usually eight spore mother cells; but some or all of these may divide again, so that the total number ranges from eight to sixteen. The further development is much like that in *Azolla*. The tapetum disintegrates, and the isolated spore mother cells are surrounded by a mass of nucleated cytoplasm.

All of the spore mother cells undergo the tetrad division, and in the microsporangium all of the spores develop. In the megasporangium, as in

Azolla, only one spore completes its development and becomes the single very large megaspore, which completely fills the sporangium.

The discharge of the spores is effected by the dissolution of the mucilaginous walls of the parietal cells of the sporangium when water is applied. No functional annulus is present, but in *Pilularia americana* it was found that the microsporangium resembled the strongly oblique sporangium of the Schizaeaceae and the terminal cells were arranged like the apical annulus of the Schizaeaceae.

The outer tissues of the ripe sporocarp, especially in *Marsilea*, are extremely hard, and impermeable; and in order to set free the spores it is necessary to break this shell. In *Pilularia* the ripe sporocarp opens spontaneously by four valves, exposing the sori, which, however, are still covered with the thick indusium.

When the hard covering of the sporocarp of Marsilea is broken, it very quickly absorbs water and the swelling of the mucilaginous inner tissues forces apart the two valves of the sporocarp; and as the swelling continues there is formed a solid gelatinous cylindrical body to which are attached the individual sori, each enclosed in a sac-like indusium. The latter soon completely dissolves and the spores are set free in the water, where they quickly germinate. Under normal conditions the development of the gametophytes in Pilularia globulifera is complete in forty to forty-eight hours; in Marsilea vestita, a common Californian species, the development of

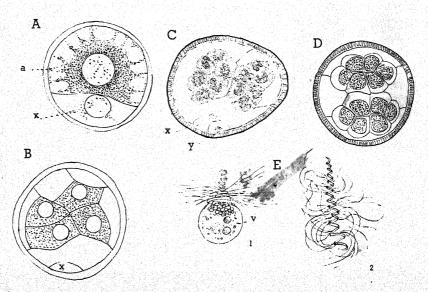


Fig. 245.—Development of the male gametophyte of Marsilea vestita; x, y, sterile prothallial cells; D, transverse section; E, spermatozoids.

the gametophytes and the fertilization are completed in less than twenty-four hours.

The gametophyte.—The first division in the germinating microspore separates a small basal cell from a much larger one, which contains most of the granular spore contents and from which the antheridia are developed. From the basal cell there is later cut off a small cell, possibly representing a rudimentary rhizoid. A similar cell is found also in the Salviniaceae.

The early divisions in the antheridial cell vary somewhat, but there result two groups of 16 spermatocytes surrounded by several sterile cells. It is probable that each of the two groups of spermatocytes represents a separate antheridium, comparable with the very simple antheridium of Schizaea.

The free spermatozoid of Marsilea is an elongated spiral filament with as many as 13 or 14 coils in M. vestita. The lower coils are much wider and partially enclose a large globular vesicle, the remains of the cytoplasm of the spermatocyte. The blepharoplast is extraordinarily developed, and the anterior coils of the spermatozoid are formed entirely from the blepharoplast. Most of the nuclear substance is found in the thickened posterior coils, but it extends into the median region, where the very numerous cilia are developed. The spermatozoid of Pilularia is much more like that of the homosporous ferns.

The large oval megaspores have very thick walls, with a mucilaginous outer coating. The large nucleus is near the apex of the spore. In *Marsilea* there is a conspicuous prominence at the apex of the spore within which the nucleus is situated. The cytoplasm surrounding the nucleus is finely granular, but the body of the spore is filled with coarsely granular materials—large starch grains, oil, and protein granules.

The first division is transverse and cuts off the apical region, which becomes the very much reduced gametophyte, consisting mainly of a single archegonium. There is some chlorophyll developed in the superficial cells, and in case the archegonium is not fertilized there may be a limited growth of the gametophyte with an increase in the development of chlorophyll. This is more marked in *Pilularia* than in *Marsilea*. The archegonium has a very short neck in *Marsilea* but one somewhat longer in *Pilularia*. There is a single neck canal cell and a small ventral canal cell.

As the gametophyte grows, the apical membranes of the spore are ruptured, and the archegonium is exposed and quickly opens. The spermatozoids collect in great numbers in the mucilage surrounding the megaspores, and fertilization is quickly effected.

The embryo.—The first division in the zygote is vertical with reference to the archegonium axis, as it is in most of the homosporous Leptosporangiatae. This division is followed by periclinal walls in the cells of the

archegonium venter, forming a two-layered calyptra; this continues to grow with the developing embryo, which remains within the calyptra until the root and cotyledon are well advanced.

The first division of the embryo in Marsilea vestita is completed within an hour after the entrance of the spermatozoid. The following divisions are the same as those in the Polypodiaceae, and the relation of the organs to each other is exactly similar.

The cotyledon in both *Pilularia* and *Marsilea* is a slender cylindrical structure with no trace of an expanded lamina. It has an axial concentric vascular bundle of very simple structure, with the tracheary tissue only slightly developed.

The stem apex is formed from one of the octants of the original stem quadrant, the sister octant developing into the second leaf, as in the common ferns. The limits of the root and foot are less clearly defined and the whole base of the young sporophyte in contact with the cavity of the megaspore containing the stored food materials no doubt functions as a haustorium. In M. Drummondii it has been shown that the nucleus of the spore cavity undergoes fragmentation, and it is quite likely that this may be the case in the other Marsileaceae.

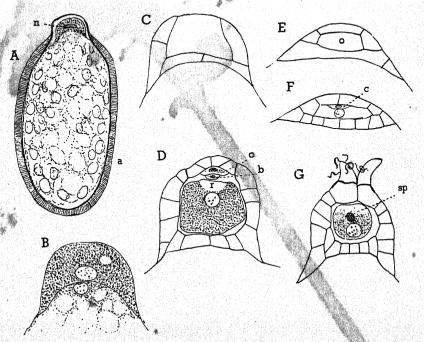


Fig. 246.—A-D, development of the archegonium of Marsilea vestita; E-F, young archegonia of Pilularia globulifera; G, open archegonium of Pilularia, showing fertilization.

The root grows vertically downward and attaches the young sporonhyte to the substratum. Its development is that of the typical ferns.

There is no essential difference between the cotyledon and the later leaves in *Pilularia* except that the early leaves do not show the characteristic circinate vernation. In *Marsilea* the awl-shaped primary leaves are gradually replaced by those with a definite spatulate lamina, which are followed by leaves with two leaflets and finally by those with the four leaflets of the adult plant.

Relationships.—That the Marsileaceae are directly related to the homosporous Leptosporang atae is obvious; and it is pretty certain that the Schizaeaceae are their nearest relatives. This is indicated by the marked similarity in the development of the sporocarp of the Marsileaceae and the fertile leaf segments (sorophore) of Schizaea. Johnson's careful study of the development of the sporocarp in both Pilularia and Marsilea confirms this. He found that the sporogenous tissue arose from marginal cells of the leaf segments which form the sporocarp, much as in the young fertile leaf segments of Schizaea, although in the latter the sporangia are solitary. The sporocarp in the Marsileaceae, therefore, may be regarded

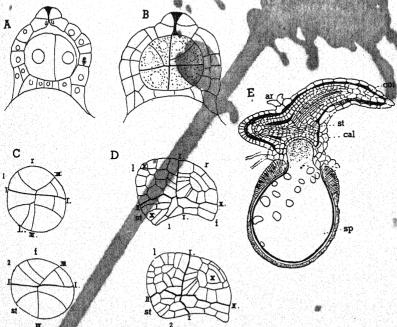


Fig. 247.—A, archegonium of Marsilea vestita, containing two-celled embryo; B, an older embryo; C, two horizontal sections of a young embryo; D, two longitudinal sections of an older embryo; st, stem; r, root; E, young sporophyte of Pilularia globulifera, attached to the megaspore, enclosed in the calvptra, cal.

as a modified "pinna" developed from the rachis of the fertile leaf. The nearest approach to this condition among the Schizaeaceae is found in Anemia, where the lower pair of pinnae are fertile and have greatly elongated stipes bearing the contracted pinnules, of which the laminae are much reduced in extent and the margins are strongly incurved so as to cover the sporangia.

The early stages of development of the sporangium in the Marsileaceae and the Schizaeaceae are much alike. While in the former there is no functional annulus, as might be expected where the discharge of the spores is effected by the action of water, nevertheless in the microsporangium of Pilularia americana, which shows the strongly oblique form typical of the Schizaeaceae, the apical group of cells closely resembles in form and arrangement the terminal annulus of the Schizaeaceae.

The anatomy of the vegetative structures in the Marsileaceae and Schizaeaceae also show striking similarities. The subulate leaves of Pilularia and the primary leaves of Marsilea have their counterparts in some species of Schizaea, e.g., S. pusilla, which grow in wet situations and have prothallia adapted to a semiaquatic environment. This might suggest a transitional condition between the terrestrial habitat of most Schizaeaceae and the amphibious condition in the Marsileaceae. The venation of the leaves in Marsilea is dichotomous like that of most of the Schizaeaceae. Finally the structure of the stele in the stem of Marsilea is like that of some of the Schizaeaceae, e.g., Anemia hirsuta. These numerous structural correspondences between the Marsileaceae and the Schizaeaceae justify the assumption of a not very remote relationship between the two families.

Of the Marsileaceae, Pilularia is the simplest and probably the most primitive. Regnellidium is intermediate and Marsilea the most specialized. Johnson believes that Marsilea is the most fern-like: but in view of the facts that the subulate leaves of Pilularia have their counterpart in some species of Schizaea and its gametophyte is less reduced than in Marsilea, we may conclude that Pilularia is the more primitive type.

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CHAPTER XVIII

HETEROSPORY AND THE SEED HABIT

The occurrence of heterospory in several quite unrelated pteridophytes must be borne in mind in studying the origin of seeds in both living and extinct plants. Of the four families of living heterosporous pteridophytes, two, Marsileaceae and Salviniaceae, unmistakably belong to the Leptosporangiatae but are not directly related to each other. These aquatic or amphibious ferns are generally placed in a special order, Hydropterides. Of the other two families, Selaginellaceae and Isoetaceae, the former is undoubtedly related to the Lycopodiaceae; but the Isoetaceae, often associated with the Selaginellaceae, in some important particulars are more nearly like the more primitive eusporangiate ferns.

In the Hydropterides the female gametophyte develops chlorophyll and may reach a relatively large size, e.g., in Salvinia. The early growth of the gametophyte is entirely at the expense of food stored in the ripe spore, which is also the case in Isoetes, where, however, there is no development of chlorophyll. The development of the gametophyte in both Hydropterides and Isoetes begins only after the spores are detached from the sporophyte. In the former the first division of the megaspore in the nucleus is followed by a cell wall, and the further development of the gametophyte is the result of repeated cell division, as in the homosporous ferns. In Isoetes, and in Selaginella before any cell walls are formed, there are many nuclear divisions resulting in numerous free nuclei distributed through the undivided cytoplasm.

In Selaginella the development of the female gametophyte begins long before the megaspore has reached its full size, and contains very little cytoplasm. The further development of the gametophyte within the megaspore depends, not upon stored food, but upon material absorbed through the tapetal cells of the sporangium which are in close contact with the growing megaspore. The developing gametophyte is therefore parasitic upon the sporophyte, thus reversing the condition found in all the other archegoniates, where the embryo sporophyte is nourished by the tissues of the gametophyte. In Selaginella apus and S. rupestris the megaspores may be retained within the sporangium until after the fertilization of the archegonium.

It is not a very long step from the condition in Selaginella to that in the primitive spermatophytes or "seed plants" where the seed is a further

elaboration of the megasporangium. The megaspore (embryo sac) remains permanently within the sporangium (ovule), and remains attached to the sporophyte until the gametophyte is completely developed and fertilization has been effected. The ovule in the lower spermatophytes is invested with a single envelope, the integument, which may perhaps be considered as an indusium, like that found in Azolla or like the "velum" about the sporangium of Isoetes. The development of the gametophyte is very much as in Selaginella, and after fertilization the ovule continues to grow, keeping pace with the development of the gametophyte (endosperm) and the embryo. In some of the lower spermatophytes the embryo sac has a thickened spore membrane like the megaspore of the heterosporous pteridophytes.

It is doubtful whether the embryo sac, in all cases, especially in the angiosperms, can be regarded as strictly homologous with the megaspore of the heterosporous pteridophytes. No cases are known where there is a tetrahedral division of the mother cell, which often may at once assume the role of the embryo sac; and whether or not the row of cells often found, one of which commonly develops into the embryo sac, can be considered a true spore tetrad is doubtful. It has even been argued that the term "heterosporous" should not be applied to the spermatophytes, as the uninucleate embryo sac may not exceed in size the microspore (pollen spore) and the term "megaspore" applied to the embryo sac is misleading. However, the same objection would apply to Selaginella, where the young uninucleate megaspore is not noticeably larger than the microspore; but this uninucleate condition can hardly be considered to be the mature megaspore, and the same might be said of the embryo sac at the time of fertilization. In both cases the megaspore is retained within the sporangium and the growth of the megaspore and the gametophyte within are dependent on material derived from the sporophyte; i.e., the gametophyte is parasitic upon the sporophyte.

The microspores (pollen spores) are much like the spores of the pteridophytes, and like them result from a regular tetra-division of the spore mother cell. The microsporangia (pollen sacs) are readily comparable with the sporangia of the pteridophytes. From the germination of the pollen spore, the male gametophyte is formed with one or two prothallial cells and a greatly reduced antheridium, in most cases producing two male gametes. In the most primitive forms, the cycads and *Ginkgo*, there are large ciliated spermatozoids comparable to those of the ferns;

but otherwise the male gametes are nonmotile.

THE SEED

The seed is a further elaboration of the megasporangium. It remains attached to the sporophyte until the enclosed megaspore (embryo sac),

which is permanently retained within the sporangium, has completed the development of the gametophyte and fertilization has been effected.

The megasporangium, or ovule, as it is called in the spermatophytes, has a central body, the nucellus, enclosed in one or two envelopes or integuments. The latter may perhaps be compared with the indusium which surrounds the sporangia in many ferns. The megasporangium of the water fern Azolla, for example, which is closely invested with a tubular indusium, is very suggestive of a simple ovule. The outer tissues of the nucellus together with the integuments later form the hard testa or seed coat, found in most ripe seeds. The embryo plant, developed from the fertilized egg cell within the embryo sac, and surrounded by the hard outer tissues of the nucellus and integuments, is very efficiently protected against external vicissitudes and can draw upon the parent sporophyte for its supply of food. Moreover, reserve food is stored in the ripe seed to be utilized in the early stages of germination. The advance of the resting stage from the unicellular spore of a fern to the completely protected embryo within the seed gives the spermatophytes a great advantage in the rapidity and certainty with which the new generation can establish itself.

That like heterospory the seed habit developed independently in several phyla is shown abundantly from a study of the Palaeozoic floras. While some of these ancient seed plants show relationships with existing types,

others appear to be without any living relations.

Throughout the Palaeozoic, from the Upper Devonian through the Permian, leaves closely resembling many living ferns are very abundant. These were long held to be true ferns; but it is now known that many of them, perhaps a majority, belonged to plants which bore true seeds. These seed ferns are now placed in a special class—Pteridospermeae or Cycado-filicales.

Another Palaeozoic order, whose relationships are very obscure, is the Cordaitales. These were trees of considerable size, showing certain structural resemblances to the living conifers, but differing from them in certain fundamental structures.

The Lycopodineae are represented by a few fossil forms bearing seeds. Lepidocarpon and Lepidostrobus are examples of Palaeozoic seeds. None of the Equisetineae (Articulatae) are known to have developed seeds.

Since it is clear that the seed habit has arisen independently in several unrelated phyla, it is practically certain that the existing spermatophytes are not all descended from a single common stock.

THE OVULE

Among living plants the seed is seen in its simplest forms in the more primitive orders—like the conifers and cycads. In these the ovules are

attached either to more or less modified "sporophylls" or are terminal on a short axis, e.g., *Taxus*, and are completely exposed so that the term gymnosperm is applied to these primitive, naked-seeded forms.

The nucellus of the young ovule in *Pinus*, for example, which corresponds to a megasporangium, is enclosed in a single integument which extends beyond the apex of the nucellus, forming a narrow orifice, the micropyle. The central region of the nucellus is occupied by a mass of sporogenous cells which develop into young megaspores. Sometimes only one of these is functional; more than one of the embryo sacs may begin to develop, but as a rule only one reaches maturity.

The development of the gametophyte is very much as in Selaginella. Many free nuclei are present, embedded in a thin peripheral layer of cytoplasm before the appearance of any division walls. Finally the embryo sac becomes filled with a compact cellular tissue, and several archegonia are developed.

In the angiosperms, the higher flowering plants, the female gametophyte in most cases has only eight nuclei and there is no definite archegonium.

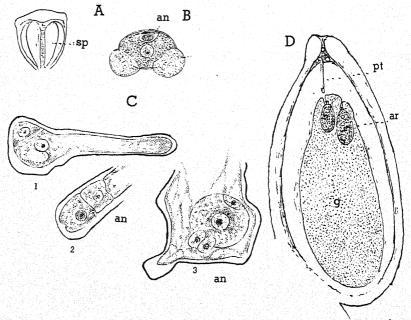


Fig. 248.—A, scale from a male cone of a pine, with two microsporangia (pollen sacs), sp; B, pollen spore of a pine, showing generative cell, an; C, germination of the pollen spore in Taxus baccata; an, antheridial cell; in C, 3, the large cell is the "body cell" of the antheridium; D, mature ovule (megaspore) of a pine; g, the gametophyte; ar, archegonia; pt, pollen tube.

The microsporangia or "pollen sacs" of the seed plants differ but little in structure from the sporangia of many pteridophytes. The pollen spores are usually formed in definite tetrads and the development of the rudimentary male gametophyte begins before the spores are shed. In most conifers the first division, as a rule, cuts off a small "prothallial" cell, which may be followed by a second one; and in *Podocarpus* and *Araucaria* the

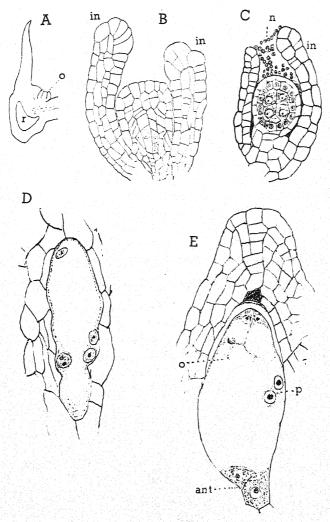


Fig. 249.—A, young ovule scale of Sequoia sempervirens; o, ovule; r, resin duct; B, section of young ovule; in, integument, and central sporogenous tissue; C, megasporangium of Azolla, suggesting an ovule; D, young embryo sac (megaspore) of Taxus baccata; E, mature embryo sac of an angiosperm (Lilaea subulata); o, egg cell; p, polar nuclei; ant, antipodoid cells.

primary prothallial cells may undergo further divisions. In other cases, e.g., Cupressus and Taxodium, no prothallial cell is formed, and this is the rule in the angiosperms. Following the formation of the prothallial cells the body of the spore is divided into a small generative cell and a large "tube cell"—the former, either directly or after a further division, giving rise to two nonmotile male gametes.

The pollen in the gymnosperms is produced in great abundance and is widely distributed by wind. Some of the pollen spores are deposited upon the ovules and sift into the micropyle, finally reaching the nucellus, where germination begins. The spore membrane is ruptured and the tube cell elongates and forms the pollen tube, into which pass the two gametes. The pollen tube penetrates the nucellus tissue covering the archegonia, very much as a fungus would do, and pushes through the neck of the archegonium and discharges the male gametes into the egg cell, where one of them fuses with the egg nucleus and effects fertilization. The resulting zygote develops into the embryo sporophyte, which generally is well advanced in the ripe seed. The development of the pollen tube eliminates the need for free water for the fecundation of the egg, and the sporophyte thus finally becomes completely emancipated from the aquatic habit inherited from its algal ancestors.

The occurrence of ciliated sperms in the cycads and in Ginkgo is the preliminary stage in this emancipation, and these ancient seed plants form a close link between the "zooidogamous" pteridophytes and the "siphonogamous" seed plants. In cycads and in Ginkgo there is formed above the apex of the female gametophyte a cavity, the pollen chamber, into which the archegonia open. The pollen spores germinate within this chamber. Part of the pollen tube penetrates the tissue of the nucellus; but the free end, which becomes greatly enlarged and gorged with fluid, finally bursts, discharging the fluid, with the large ciliated gametes, into the pollen chamber, where fertilization is effected very much as in the ferns. A similar development of a pollen chamber has been found in the seeds of some Palaeozoic pteridosperms and Cordaitales, but no pollen tubes have been discovered in these forms.

As the seed develops, the outer tissues become hard, forming the "testa" or seed coat, and the cells of the gametophyte in which the embryo is embedded are filled with reserve food. This gametophytic tissue is the "endosperm" of the ripe seed. Protected within the seed, the dormant embryo may remain alive for an indefinite period—ready to start growth when conditions are suitable. The seed represents three generations. The outer tissues belong to the original sporophyte; the gametophyte (endosperm) within the embryo sac is the true sexual generation, and the embryo forms the second neutral generation or sporophyte derived from the fertilized egg.

While there is much variation in the details of the seeds of different plant types, the essential structure is alike in all of them. A section of the ripe seed in many cases shows the embryo lying in a mass of endosperm cells filled with reserve food. In the gymnosperms the endosperm is the primary gametophyte which fills the embryo sac; in the angiosperms the endosperm is a secondary structure. The testa is derived from the outer tissue of the nucellus and the integument. Among the angiosperms, in many cases, the endosperm is used up by the developing embryo, which may completely fill the embryo sac in the ripe seed—e.g., bean, melon. In such cases the fleshy primary leaves, or cotyledons, contain the stored reserve food. The dry seed in some cases may remain dormant for many years but under proper conditions will germinate the embryo, sending a root into the ground, and, discarding the remains of the seed coat, assumes the role of an independent plant.

THE FIRST SEED PLANTS

The oldest known seed plants occur in the Upper Devonian. The most remarkable is *Eospermatopteris textilis*, found in Devonian rocks in eastern New York. It was of tree-like proportions and probably resembled in habit the modern tree ferns, and is one of the pteridosperms, already referred to.

So far as is known, the Equisetineae (Articulatae) never attained to seed formation, although evidence of heterospory of a simple type has been found in some species—e.g., Calamostachys Cashiana. Among the Lycopods, however, aside from Selaginella, there are several cases of heterospory among the fossil forms, as well as true seeds. In Lepidocarpon the seed has a definite integument, with a micropyle, but no pollen chamber; and the method of fertilization is not clear.

All of the Palaeozoic seed plants—as well as their nearest living relations, cycads, conifers, and Ginkgo—have the ovules completely exposed and not contained in the closed "ovary" characteristic of the higher "flowering" plants—the angiosperms—predominant in modern floras. The Palaeozoic spermatophytes were all gymnosperms; but this does not imply that they all belonged to a common stock. It is evident that the existing gymnosperms represent several divergent lines of development the relationships of which with each other—if any—and to the different groups of Palaeozoic seed plants are very obscure.

Two orders of living gymnosperms, Cycadales and Ginkgoales, are the most ancient and can be traced back to the Permian and possibly to the Late Carboniferous. They are probably descended from forms related to the pteridosperms and retain marked evidences of their fern ancestry. In view of the similarity of the ovules of some of the pteridosperms to those

of the cycads it is extremely likely that in these Palaeozoic gymnosperms also, fertilization was effected by active spermatozoids.

Of the existing gymnosperms the conifers are by far the most abundant and in some regions, like the Pacific Coast of North America, are the dominant forest trees. Up to the beginning of the Cretaceous the spermatophytes—at least so far as revealed by the fossil record—were gymnosperms; but in the Lower Cretaceous there are found remains of trees and shrubs closely resembling living genera—like the sycamore (*Platanus*), sassafras, and poplar, members of the now predominant angiosperms. From the highly specialized character of these Cretaceous angiosperms, it is obvious they must have been preceded by a long series of more generalized ancestors, and there has been much speculation as to the nature of these predecessors of the modern flowering plants.

Recently some peculiar fructifications were discovered in Jurassic rocks with seeds borne in closed receptacles. These angiospermous fructifications have been made the type of a special order, Caytoniales. Whether or not these are related to the existing angiosperms is questionable, and it is to be hoped that further research may reveal other Jurassic fossils which may throw some light upon the origin of the now dominant angiosperms.

PTERIDOSPERMS

Throughout the Palaeozoic from the Upper Devonian to the Permian, leaves closely resembling those of living ferns are very abundant. The greater part of these are sterile fronds only, and their relationships were very uncertain. Some of these leaves were associated with stems which showed secondary growth of the vascular bundles, like the stem structure of the cycads, rather than true ferns. On the basis of these anatomical characters Potonié proposed to establish a definite order, "Cycadofilicales," for these forms. Somewhat later it was discovered that true seeds were associated with some of these Cycadofilicales, and the name Pteridospermae was suggested to replace that of Cycadofilicales. It is now evident that a large part of the supposed ferns of the Palaeozoic were really pteridosperms. These seed-bearing ferns have been extensively studied especially by British botanists and by many investigators in Europe.

The oldest seed plants known are found in the Upper Devonian. The most remarkable of these was *Eospermatopteris*, already referred to, discovered in eastern New York state. In 1869 a freshet exposed a veritable forest of large fossil stumps, some more than two feet in diameter. About ten years ago these were carefully investigated and restorations were made to show their probable appearance. These restorations indicate that *Eospermatopteris* resembled in habit living tree ferns, from which, however,

it differed in some important particulars. The base of the trunk formed a large bulbous body, presumably buried in the soft soil of a swampy area where it was inferred the trees grew. There were no large roots, but remains of many very slender ones were abundant.

The trunk tapered gradually, possibly to a height of ten meters or more, and bore a crown of large tripinnate fronds, the final divisions of which were narrow and dichotomously branched like those of the Psilophytales. Some of the pinnae bore at the apex of the ultimate divisions small oval bodies which were shown to be simple seeds having a single envelope—presumably an indusium representing a single integument of the ovule. Microsporangia (pollen sacs) were found on other fronds but were not sufficiently well preserved to show clearly their structure. The absence of large roots and the dichotomous branching of the ultimate leaf divisions, as well as the position of the sporangia, are reminiscent of the Psilophytales and make it possible that Eospermatopteris and perhaps other pteridosperms were derived directly from the Psilophytales rather than from true fern ancestors.

It is not always possible to decide whether the very numerous fern-like fronds that abound in the Palaeozoic rocks, from the Devonian onward, belong to true ferns, pteridosperms, or cycads; and it may be assumed that the pteridosperms do not form a closed phylum, but that seeds developed in several lines of fern-like plants. It is not likely, therefore, that all the later seed plants were derived from the same Palaeozoic ancestors.

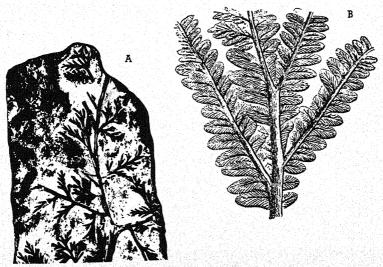


Fig. 250.—Pteridosperms. A, Heterangium Grieri (= Sphenopteris elegans); B, Callipteris conferta (A, after Gothan; B, after Potonié).

The classification of the pteridosperms, owing to the very imperfect knowledge of the structure of most of them, must necessarily be for the present a tentative one. Scott, who has contributed much to our knowledge of the pteridosperms, makes two major groups, Lyginopterideae and Medulloseae.

Lyginopteris oldhamia, the best-known species, is a common fossil of the British lower and middle coal measures. The ample fern-like leaves of the Sphenopteris type were spirally placed upon an elongated slender stem, forming a marked contrast to the massive trunk of Eospermatopteris, although their foliage was similar. Of the numerous genera placed provisionally in the Lyginopterideae, Heterangium is one whose structure has been carefully investigated. The fern-like fossil Sphenopteris elegans is thought to belong really to Heterangium. The stem of Heterangium in the young plant had a solid central vascular cylinder (protostele) in which were numerous groups of tracheids surrounded by parenchyma. In the older stems there is a cylinder of secondary wood developed from a zone of cambium outside the primary xylem.

In Lyginodendron, instead of the solid protostele of Heterangium there is a central pith, which Scott concludes replaced the protostele. Surrounding the pith in the young stem is a circle of isolated vascular strands which are connected directly with the bundles of the leaf petioles—that is they are "common" bundles such as occur in the Eusporangiatae and are also characteristic of most angiosperms.

The leaves of Lyginopteris, like those of Heterangium, have been described as species of Sphenopteris. The stalk of the frond divided into two equal branches, which were pinnately compound. The rachis is traversed by a single concentric vascular bundle which in cross section is V-shaped and structurally is like that of the typical ferns.

The seed.—The seed in Lyginodendron, described originally under the name Lagenostoma, like that of Eospermatopteris is borne at the tips of the divisions of the fertile fronds. Also like the latter they were enclosed in a conspicuous envelope, the exact nature of which is still doubtful. It has been compared with the "cupule" of a hazelnut or acorn but might perhaps be equally well compared with the fleshy "aril" surrounding the seed in the yew. It may also be interpreted as an outer integument. The primary integument is completely coherent with the nucellus except at the apex, where it forms a narrow opening, the micropyle, into which the apex of the nucellus extends as a beak. Within the apex of the nucellus an open cavity, the pollen chamber, is formed, opening into the micropyle and permitting the entrance of the pollen spores. The formation of the pollen chamber is much like that found in the ovules of the cycads, and

Lyginodendron also resembles the latter in the extension of the vascular bundles into the integuments.

The structure of the female gametophyte within the megasporangium has not been sufficiently preserved to throw much light upon it; but analogy of it with that in *Selaginella* and the living gymnosperms makes it pretty certain that there were well-developed archegonia opening into the pollen chamber.

Microsporangium.—The occurrence of sporangia associated with various fern-like Palaeozoic fossils has long been known, and these were supposed to be homosporous sporangia, some of them belonging to Marattia-

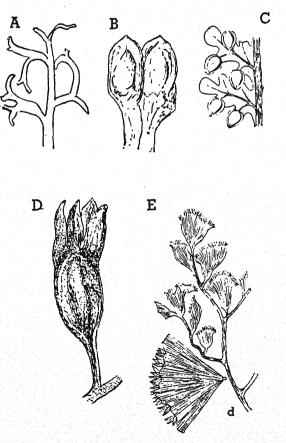


Fig. 251.—Fructifications of pteridosperms. A, segment of sterile frond of Eospermatopteris textilis; B, two seeds of Eospermatopteris; C, seeds of Pecopteris Pluckeneti; D, seed of Lagenostoma Sinclairi; E, Potoniea adiantiformis, with microsporangia (A, B, after Goldring; C, Scott, after Teiller; D, Scott, after Arber; E, Scott, after Bertrand).

ceae. In 1905 Kidston showed that one of these, Crossotheca, associated with Sphenopteris, was really the microsporangium of Lyginopteris. Other similar cases have been noted; but it is still uncertain how large a proportion of these sporangia really belongs to pteridosperms rather than to true ferns.

The sporangia of *Crossotheca* are fusiform-pointed bodies, pendent from the margin of discoid sporangiophore formed from the fertile segments of the *Sphenopteris* frond. The sporangium has two loculi. The sporangiophore with its pendent sporangia recalls *Equisetum*.

The microspores themselves have been found within the pollen chamber of the ovule, and there has even been found a multicellular body within the spore like that in the germinated microspores of the heterosporous pteridophytes. There is no evidence of a pollen tube; and it is possible that the spermatozoids were discharged directly from an antheridium into the fluid presumably filling the pollen chamber.

MEDULLOSEAE, NEUROPTERIDEAE

Certain fern-like fossil fronds, of which the commonest are Neuropteris and Alethopteris, have been placed in a common group, Neuropterideae, and are often associated with large petrified stems in the Carboniferous and Permian, among which the genus Medullosa has been most completely studied, especially by Scott. Some of these had stout upright trunks covered with the sheathing leaf bases recalling the Marattiaceae, with which the anatomical structure of the stem also shows important resemblances.

The stem anatomy of *Medullosa* recalls that of many true ferns, as there are numerous separate concentric bundles; but unlike most of the existing ferns, the bundles show the formation of secondary wood, much as in *Lyginopteris*. There is a massive cortex within which are conspicuous canals resembling the mucilage ducts of the Marattiaceae and found also in the cycads.

The fossil fronds that have been referred to the Medulloseae belong mostly to the Neuropterideae. These fronds are often of great size and are several times pinnate. In *Neuropteris* the leaflets are ovate or oblong, with broad base and sometimes a short stalk. There is a definite midrib, which toward the apex of the leaflet divides dichotomously into several fine veinlets. The numerous lateral veins are also dichotomously branched. Scott compares the venation to that in *Osmunda*. The structure of the stout petiole corresponds with that of the leaf bases of *Medullosa*.

Seeds.—Only a very small number of seeds have been found that can certainly be assigned to the Medullaceae. Scott cites two cases where rather large seeds have been found attached to the tip of little-modified pinnules of Neuropteris heterophylla and N. obliqua.

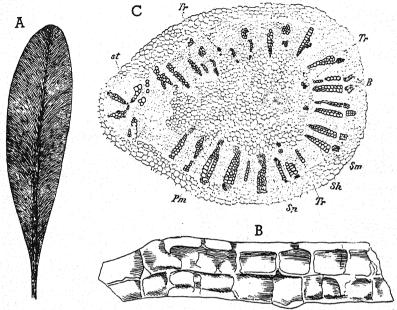


Fig. 252.—A, Glossopteris Browniana; B, Vertebraria indica (rhizome of Glossopteris); C, section of stem of Medullosa stellata (A, B, Gothan, after Feistmantel; C, after Gothan).

GLOSSOPTERIDACEAE

In the Late Palaeozoic formations of many parts of the Southern Hemisphere regions associated with the ancient "Gondwana Land," there occur in great numbers impressions of a very peculiar kind, of which Glossopteris is the type. There are a number of other characteristic genera in this "Glossopteris flora." These are quite unknown in corresponding formations in North America and Europe but have been found in northern Russia and Siberia.

The leaves of Glossopteris were tongue-shaped, with a well-marked midrib and very numerous reticulate veins. In some cases on either side of the midrib a row of dots was observed which may possibly have been the remains of sori. Seward (Plant Life through the Ages, pp. 242, 243) states that although no seeds have been found in situ, seeds are often found associated with the leaf impressions; and he concludes that Glossopteris was a pteridosperm.

During the closing period of the Palaeozoic there was an extensive glacial period in the Southern Hemisphere, and it is supposed that the Glossopteris flora developed during relatively cold conditions. Fossil remains of Glossopteris have been collected in Antarctica within 300 miles of the pole (Seward, op. cit., p. 243).

The relationships of the pteridosperms.—There are various theories as to the origin and relationships of the pteridosperms. That they are allied in some degree to the true ferns is practically certain; but that they have originated from ancestors comparable to the living ferns is another matter. The remarkably fern-like foliage, together with their anatomical characters, makes it very unlikely that these similarities are purely homoplastic.

The discovery of pteridosperms in the Late Devonian and Early Carboniferous indicate that their pteridophytic ancestors must have existed much earlier. There are no evidences that ferns of the modern type existed at this time; but from the Devonian onward primitive ferns, Coenopteridaceae, Archaeopteris, etc.—the "Primo-filices"—did exist; and these show evidences of relationship with the Psilophytineae, from which the primitive ferns were presumably descended. It seems therefore probable that from some common stock derived from the Psilophytineae there developed various lines, some leading to the typical homosporous ferns, others developing heterospory and later seeds, resulting in the pteridosperms; but it is hardly likely that the latter comprise only a single closed phylum.

Scott's conclusion that the pteridosperms should constitute a special class, co-ordinate on the one hand with the Filicineae on the one hand and with all the gymnosperms on the other, seems hardly justified. It would seem more in accordance with the known data to rank them as an order—perhaps "Cycadofilicales," as Coulter and Chamberlain propose—an order which may be considered either as the most advanced of the Filicineae or the most primitive of gymnosperms.

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CHAPTER XIX

GYMNOSPERMS—CYCADOPHYTA (CYCADALES, BENNETTITALES)

It is evident that the seed habit was well established in later Palaeozoic time, and it is clear that seeds were developed independently in several phyla. As we have already seen, the two most important of the Palaeozoic seed plants were the pteridosperms, or Cycadofilicales, and the Cordaitales. They show a number of marked structural resemblances, which indicate a certain degree of relationship; and each of these orders shows a similar suggestion of relationship with some of the existing gymnosperms, but neither pteridosperms or Cordaitales have left any recognizable descendants in the later geological formations.

Of the Palaeozoic seed plants the Cordaitales most nearly approach in structure the most primitive of the existing gymnosperms, but there is little reason to conclude that any of the latter are direct descendants of Cordaitales. Our knowledge of the reproduction in the Palaeozoic seed plants is too incomplete to make a satisfactory comparison with that of the living spermatophytes. Some of the Palaeozoic seeds have been compared with those of the cycads and of Ginkgo, the most primitive of the living gymnosperms. Like the latter, the ovules of the Cordaitales and some pteridosperms, e.g., Lagenostoma, developed a pollen chamber, indicating that fertilization was effected by motile sperms; but none of the Palaeozoic forms have as yet shown evidences of the formation of a pollen tube—a condition found in all living seed plants.

In the Late Carboniferous and Permian, numerous fossils occur which show marked resemblances in structure with some of the living gymnosperms, although none of them can be certainly assigned to any living genera. During the Mesozoic these primitive gymnosperms became more and more abundant, and in the Early and Middle Mesozoic, where they became the predominant plant types and include some genera that have persisted to the present time. Toward the end of the Mesozoic, during the Cretaceous, gymnosperms gradually give way to angiosperms, the dominant modern type of "flowering plants," which, from the Cretaceous onward, comprise the great majority of seed plants. At present only about five hundred species of gymnosperms survive; but these include the giants of the vegetable kingdom.

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CLASSIFICATION OF GYMNOSPERMS

The existing gymnosperms are divided into four orders, viz., Cycadales, Ginkgoales, Coniferales, and Gnetales. The first two are very natural groups, each with a single family; but the members of the other two orders show much greater diversity, and their interrelationships are by no means always clear.

ORDER CYCADALES

The Cycadales include about 85 living species, all referable to a single family, Cycadaceae. These are the sole survivors of the once extensive group of cycadophytes, which were characteristic of the Mesozoic era and dominated the vegetation during much of the Mesozoic. Our knowledge of the Cycadaceae has been greatly advanced through the researches of a number of American botanists, especially Dr. J. C. Chamberlain.

The cycads, the most primitive of the living seed plants, show striking similarities in structure to the more primitive ferns. Their general habit, especially the leaves and some anatomical structures, recall the Marattiales and Osmundaceae, which are represented in the later Palaeozoic. One group of the pteridosperms, the Medulloseae, show some notable resemblances to the cycads. The development of large ciliated spermatozoids is especially suggestive of their filicinean relationship. It is not likely that the living cycads are direct descendants of either Marattiales or Medulloseae, but there can be little doubt that they are remotely related to both of these.

Abundant fossil remains of foliage and stems of cycadean type are known, and it was assumed that this was evidence of the existence of true cycads in the later Palaeozoic; but sporangia or seeds that can be definitely assigned to Cycadaceae have not been found before the Triassic; and at present it is impossible to say when the first true cycads appeared.

Many of the supposed cycadean fossils are now known to belong to another order, Bennettitales, or *Cycadeoidea*, which were very abundant during the Mesozoic, and presumably were associated with many true cycads, which they closely resemble in their general habit and anatomical characters but from which they differ greatly in their reproductive structures. The problem here is comparable with that of the ferns and pteridosperms of the Palaeozoic.

The Bennettitales probably greatly outnumbered the true cycads, and show a much greater range of structure. They were apparently the predominant seed plants of the Mesozoic and have been thought to have played a role in the Mesozoic floras, comparable to that of dicotyledons in the modern world. Just what degree of relationship existed between Cycadales and Bennettitales it is impossible to decide, but that the orders

were entirely unrelated is hard to believe; their inclusion in a common class, Cycadophyta, seems warranted.

In the Triassic and the Rhaetic remains have been found of both male and female sporophylls which have been assigned to Cycadales but can hardly be considered closely related to any of the living Cycadaceae. Fertile ovulate fronds (Cycadospadix), much like those of the genus Cycas, occur in the Rhaetic and the Jurassic, and possibly in the Upper Triassic.

While the geological evidence of the Cycadales is very incomplete, their structure indicates that they are the most primitive of the existing gymnosperms. Their general morphology and anatomy have much in common with the eusporangiate ferns, especially the Marattiaceae, and this is true also of the sporangia. Together with *Ginkgo*, known to be also a very old type, cycads alone retain the motile spermatozoids characteristic of the pteridophytes.

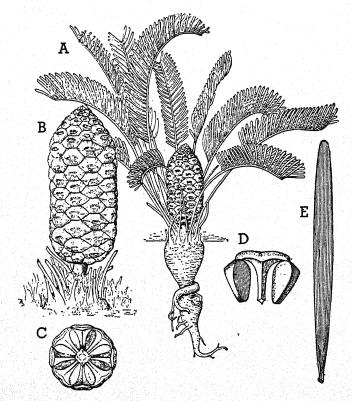


Fig. 253.—A, Zamia floridana, plant bearing an ovulate strobilus; B, strobilus; C, cross section of strobilus; D, a single scale with two seeds; E, single pinna of leaf, showing venation (all figures after Wieland).

Peculiar among living gymnosperms, the cycads retain the fern-like habit with the ample compound, pinnate fronds of the true ferns. Cycas and some other genera have the young leaves with coiled segments like those of the ferns. The leaves of Stangeria so closely resemble the leaves of Lomaria, a fern, that the plant was first referred to that genus.

An argument for the antiquity of the Cycadales is their distribution, which is very significant. Of the nine recognized genera five belong to the Eastern Hemisphere and four to the Western. Except for Cycas, which occurs in the eastern tropics from Japan to Australia, the other eastern genera are confined to South Africa and Australia, while in America they are mostly restricted to Mexico and the Caribbean regions. Mexico, South Africa, and Australia are all old stable regions; and although the last two may have been included in "Gondwana Land," there is no evidence of any more recent connection between these and the Mexican areas, while there is no question that the cycads of these widely separated regions are related and must have been differentiated as such at some very early period. These two groups are doubtless relicts from some remote period, perhaps the Jurassic, when the cycads had a worldwide distribution.

All of the living cycads are sufficiently alike to warrant their inclusion in a single family, Cycadaceae, which, however, has been divided into several subfamilies. Pilger, who has described the Cycadaceae in the Engler and Prantl Natürlichen Pflanzenfamilien, recognizes five subfamilies: (1) Cycadioideae; (2) Stangerioideae; (3) Bowenioideae; (4) Dioonioideae; (5) Zamioideae.

The first four subfamilies are each represented by a single genus; but Zamioideae, which includes the majority of the species, has five genera: Zamia, Encephalartos, Macrozamia, Microcycas, and Ceratozamia.

The cycads may have a stout columnar trunk with a crown of pinnate leaves, recalling a tree fern or palm. The so-called "sago palm," often seen in conservatories, is a cycad, Cycas revoluta. An Australian cycad, Macrozamia Hopei, may reach a height of 20 meters. In other cases, like the two species of Zamia, found in Florida, the only representatives in the United States, they are dwarf forms with subterranean tuberous stems resembling in habit a fernlike Osmunda. There is, however, a very marked difference. Instead of the numerous, relatively slender roots of the fern, there is a massive taproot like that of the conifers.

The arborescent forms, like Cycas and Macrozamia, differ in the development of the leaves from the palms which they resemble superficially and recall many ferns, like Osmunda or Asplenium, which develop a single cycle of new leaves each season. The trunk is covered with the closely set leaf bases, which persist after the leaves are shed, a condition also found in the Marattiaceae. There may be in some cases a dichotomy of the apex

or lateral branching, but the branching is not usual and is very different from the extensive branching of the conifers and *Ginkgo*.

The cycads are dioecious, ovules and pollen sacs being developed on separate individuals. In Cycas the ovules are borne on the margins of sporophylls, which, though smaller than the sterile leaves, have a definite pinnate structure. In all the other genera the ovular sporophylls are much reduced in size and form a solid cone or strobilus, and there are only two ovules on each sporophyll. The numerous pollen sacs, or microsporangia, are situated on the lower surface of the thick, wedge-shaped sporophylls, which in all the genera form a large strobilus. The pollen sacs are structurally much like the sporangia of the eusporangiate ferns. They cover the greater part of the lower surface of the sporophyll, are grouped in crowded sori, but are not united into a synangium.

Of the eastern cycads, Cycas has the widest distribution, ranging from southern Japan to northern Australia and occurring also in Madagascar and Polynesia. Stangeria is confined to South Africa, while Macrozamia and Bowenia are found only in Australia. Encephalartos also reaches tropical Africa. In America, Zamia is the largest genus, including two species in Florida. Other species range from the West Indies and Central America to northern Brazil and Bolivia. Microcycas is known only from Cuba, while Dioon and Ceratozamia are Mexican.

The stem.—While in most of the cycads a massive trunk is formed, in Zamia, Bowenia, and Stangeria the stem is a thick tuber, sometimes suggesting a large turnip or radish and almost completely subterranean. In these genera the whole leaf is shed and the stem is not covered with the persistent leaf bases found in the arboreal types.

The woody tissue of the stem is much less developed than in the conifers and the Ginkgoales, and there is a corresponding increase in the size of the pith and cortex. In both of these there occur conspicuous mucilage ducts, very much like those in the Marattiaceae. The large pith is surrounded by a ring of collateral vascular bundles having active cambium from which secondary wood is formed, much as in the pteridosperms and the Cordaitales, and in the conifers. This cambium may persist, resulting in a continuous but slow increase in the thickness of the woody cylinder of the stem. In *Cycas* the activity of the primary cambium is limited and a succession of secondary cambium rings arises in the cortex, which form more or less regular zones of vascular bundles having the concentric structure of those of the typical ferns.

The bundles constituting the woody cylinder anastomose and form a network, the spaces being the medullary rays through which the leaf traces pass out into the cortex. The leaf trace divides into two branches before it joins the leaf base.

In some of the cycads, e.g., *Encephalartos* and *Macrozamia*, an independent system of bundles is found in the pith. These seem to be true cauline structures and may be compared with the commissural strands of the Marattiaceae. Similar medullary bundles occur in the fossil Medulloseae.

The first-formed xylem elements are scalariform tracheids like those of the ferns. Later tracheids have crowded bordered pits like those of typical coniferous wood.

The growth of the woody cylinder is very slow and usually no definite growth rings can be recognized; but extremely narrow growth rings have been found in *Dioon spinulosum*, which has the most massive woody cylinder of any known cycad.

Leaves.—The leaves in all genera except Bowenia are simply pinnate, and firm and leathery in texture. In size they range from 5 or 6 centimeters in Zamia pygmaea to 3 meters in Cycas circinalis. Where the stem is subterranean the leaves are few and formed in succession. In the larger forms like Cycas and Ceratozamia a complete new crown of leaves is produced periodically, very much as in many ferns. Alternating with the crowns of foliage leaves there is in most cases a series of thick scale leaves. The younger parts of the crown are often covered with masses of hairs, thus resembling some of the tree ferns, e.g., Cibotium.

The pinnae of the leaf are generally narrow with entire margins; but

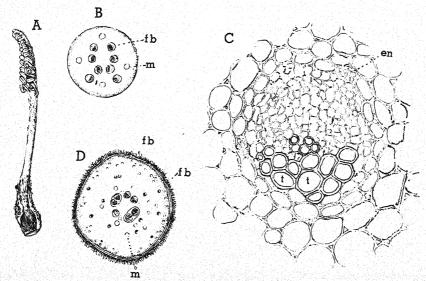


Fig. 254.—A, young leaf of Cycas revoluta; B, cross section of petiole of older leaf; C, vascular bundle of petiole; en, endodermis; D, section of peduncle of cone of Zamia integrifolia; m, mucilage ducts.

sometimes, e.g., Encephalartos, Dioon spinulosum, there are more or less conspicuous teeth. In Macrozamia heteromera, the pinnae are dichotomously cleft. The pinnae in Cycas have a thick midrib but no lateral veins. Stangeria also has a midrib, but there are numerous lateral veins and the leaves resemble closely those of the Marattiaceae, especially Danaea and Macroglossum. In the other genera there is no midrib and the venation is of the cyclopterid type. There is a repeated dichotomy of the veins at the base of the pinnule resulting in numerous parallel veins, much like the venation of Cordaites. Bowenia has long-stalked leaves, bipinnate, arising from the subterranean rhizome; and the form of its leaf recalls the common bracken. The parallel venation of the pinnules is like that of most of the other cycads.

There are two leaf traces which enter the base of the rachis, and these fork within the petiole and extend into the pinnae. In Cycas the bundles of the petiole are collateral; but the phloem is on the inner side of the bundle and the xylem on the outer side. The cells of the epidermis are strongly cutinized and there is a well-developed hypoderma. Below the hypoderma is a palisade layer and below this the more or less spongy mesophyll. The stomata are confined to the lower epidermis and are sunk in pits, like those of the conifers. In leaves with parallel venation the bundles are connected by bridges of peculiar parenchyma cells, a condi-

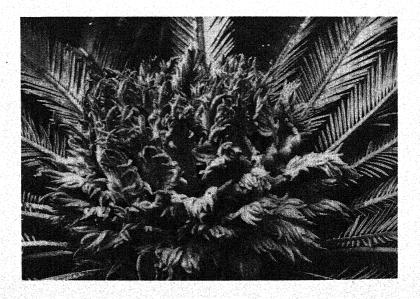


Fig. 255.—Megasporophylls of Cycas revoluta

tion also found in the Cordaitales. Like the stem, the petiole contains conspicuous mucilage ducts.

The root.—The primary root of the seedling persists as a massive taproot, which usually develops numerous lateral secondary roots. They may occasionally branch dichotomously. A dichotomy of the primary root has been noted in Stangeria. A peculiarity of the secondary roots of the cycads is the occurrence in some of them of irregular tubercular masses at the surface of the ground. The formation of these tubercles is associated with the presence of an endophytic alga, Anabaena, and recalls the association of similar blue-green algae with Azolla and the Anthocerotaceae. With the Anabaena are found bacterioid organisms like those in the tubercles formed on the roots of many Leguminosae. It is thought these tubercles may be concerned in nitrogen fixations, or perhaps with aeration of the roots.

Reproduction.—Except in Cycas, where the sporophylls bearing the ovules are arranged in a loose crown around the stem apex the sporophylls form a definite strobilus, which is developed from the apex of the shoot, whose further growth is thus stopped. Later a new stem apex is formed, so that the apparently unbranched trunk is really a sympodium. In En-

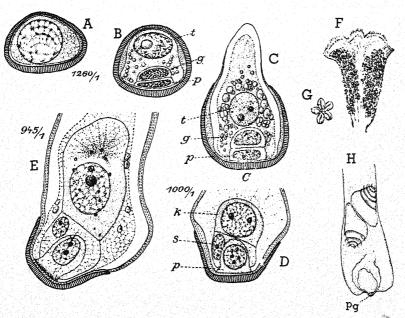


Fig. 256.—A-E, development of the male gametophyte of Dioon edule; t, tube nucleus; p, prothallial cell; g, generative cell; s, stalk cell; k, body cell; F, scale from male cone of Cycas revoluta; C, microsporangia (pollen sacs); H, pollen tube of Zamia integrifolia, containing two spermatozoids (A-E, Pilger, after Chamberlain; H, after Webber).

cephalartos, however, the strobili do not involve the stem apex but are formed on lateral shoots.

The microsporophyll in *Cycas* is a thick, wedge-shaped body, the outer end bent upward and tapering to a point. The lower surface is closely set with the numerous pollen sacs which are grouped in more or less definite sori, like the sporangia of certain ferns, e.g., *Platycerium* and *Todea Barbara*.

The structure of the microsporangium is much like that of Angiopteris or Macroglossum of the Marattiaceae, in which the sporangia are not united into a synangium. The wall of the pollen sac is composed of several layers of cells and there is a central mass of sporogenous cells. The tapetum is less developed than in the Marattiaceae. It is sometimes derived from the archesporium (Stangeria, Zamia); but in Dioon Chamberlain states that it is derived from the inner parietal cells, as it is in the Marattiaceae. The dehiscence, by a vertical cleft, is the same.

The pollen spores are small and their number may be very great. Thus Chamberlain estimated the number for *Dioon edule* as 30,000. Zamia has the smallest output, 500–600.

Germination of the pollen spore begins within the sporangium. A small prothallial cell is cut off like that in *Selaginella*; from the large antheridial cell another small cell is cut off; and the pollen spore, when set free, has three cells.

The foliar nature of the megasporophyll of Cycas is very evident and indicates a more primitive condition than that of the other genera where the sporophyll is greatly reduced in size. There is an interesting series in the genus Cycas, from C. revoluta, where the sporophyll has a large lamina with elongated pinnae and several marginal ovules, to C. Normanbyana, where the lamina is greatly reduced in size and the ovules are usually reduced to a single pair, the typical number in all the other genera. C. Rumphii and C. circinalis are intermediate types. In some of the strobiloid genera, e.g., Stangeria and Dioon, the megasporophyll, while smaller than in Cycas, has an expanded, leaf-like apex; but in the most specialized genera, Zamia and Ceratozamia, the foliar character is quite lost and the outer ends of the sporophylls are flattened and much thickened, forming closely fitting, hexagonal shields suggesting the cone of Equisetum. The full-grown strobilus is sometimes very large. Chamberlain gives a figure of a cone of Macrozamia Denisoni from Queensland which was 37 inches long and weighed 85 pounds (Chamberlain, Gymnosperms, Fig. 94). The seeds also reach large size; in Cycas circinalis the ripe seed is as large as a small hen's egg.

The ovule has a massive integument, which is coherent with the nucellus except at the apex, where it extends beyond the free apex of the nucellus,

leaving a narrow space which communicates with the exterior through the micropyle. The integument finally shows a differentiation into three layers, an outer and an inner fleshy one, between which is a layer of extremely hard, stony tissue (sclerenchyma). In each of the fleshy layers is an independent system of vascular bundles, and it is sometimes held that this indicates that there are really two coalescent integuments. The structure has been compared to that in the fossil *Lagenostoma*, a pteridosperm with an ovule much like that of the Cycadaceae.

The earliest stages of the embryo sac are still incompletely known. Lang describes in *Stangeria* the presence of a row of three cells, of which the lower becomes the embryo sac. In *Zamia floridana* Dr. F. Grace Smith found a similar row of four cells, which are considered to represent four megaspores, of which the lowest becomes the embryo sac. This is much like the condition in some of the Coniferales and also in many angiosperms. At what point the reduction division occurs is not clear, and whether or not the row of four cells in *Zamia* really represents a spore tetrad might be questioned.

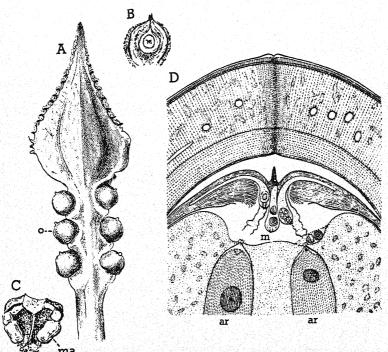


Fig. 257.—A, megasporophyll of Cycas Rumphii; o, ovules; B, section of young ovule of Cycas revoluta; C, sporophyll of Zamia integrifolia with two ovules, ma; D, apex of ovule of Dioon edule, showing pollen tubes in the pollen chamber (D, Pilger, after Chamberlain).

The nucleus of the embryo sac divides repeatedly until there is a large number of free nuclei, very much as in Selaginella and Isotes. As noted above, the point at which the reduction division occurs is not clear, but the free nuclei in the embryo sac are presumably haploid. The embryo sac rapidly increases in size, and there is formed a large central vacuole surrounded by a layer of cytoplasm containing many free nuclei, a condition not unlike that in Selaginella. Later, cell walls form between the nuclei, and finally the embryo sac becomes filled with cellular tissue, constituting the female gametophyte. Several archegonia are developed at the apex of the gametophyte. The archegonium is more reduced in structure than in any pteridophytes. It consists of two small neck cells and a very large central cell. Before fertilization the nucleus of the central cell divides into two-a very large one, belonging to the egg cell, and an inconspicuous "ventral canal nucleus," which is difficult to demonstrate. The absence of a definite ventral canal cell recalls the condition in some of the Eusporangiatae, e.g., Ophioglossum and Danaea, where a ventral canal cell has not been certainly demonstrated.

Although the megaspore (embryo sac) is retained permanently within the ovule it possesses a distinct spore membrane, a condition found also in *Ginkgo*. The egg cell increases greatly in size and its cell wall becomes much thickened with the formation of pits, into which papillae, or haustoria, extend, through which food from the surrounding gametophytic tissue is conveyed to the growing egg cell.

Before the archegonia are formed, the apical region of the nucellus forms a beak, which is pushed up into the micropyle. Within this beak the tissues are broken down, leaving a cavity, the pollen chamber, into which the pollen grains are forced.

Professor Chamberlain's detailed study of fertilization in *Dioon edule*, a Mexican cycad, illustrates the process of fertilization in the Cycadaceae. When the pollen grains are carried by the wind, and fall upon a receptive ovule, they are held by a drop of fluid which exudes from the micropyle. With the evaporation of the fluid, the pollen spores are sucked into the micropyle and forced into the pollen chamber, into which the archegonia later open.

The pollen spores are very small and the development of the male gametophyte is slow, about six months elapsing in *Dioon* between pollination and fertilization. The pollen tube forms from the upper part of the spore and bores its way into the tissue of the nucellus very much as a fungus hypha would do. The pollen tube thus serves as a haustorium drawing from the nucellar tissue nourishment for the development of the male gametophyte. The pollen spore when shed has three cells, viz., the prothallial cell, the generative cell, and a tube cell.

Very soon after germination begins the generative cell divides into two—the "stalk cell" in contact with the prothallial cell, and the "body cell." Within the latter, two blepharoplasts arise, showing characteristic radiations like the centrosomes of many animal cells and those of some brown algae and certain Hepaticae. The body cell divides into two spermatocytes, each with a large nucleus and blepharoplast. According to Cham-

berlain the large spermatozoids are discharged from the spermatocytes, from which they later escape into the pollen tube.

The development of the spermatozoids resembles that of the Ophioglossaceae and Marattiaceae, but the nucleus is enormously larger and retains its globular form. The blepharoplast breaks up into granules, which fuse to form the large blepharoplast, which is coiled spirally about the nucleus and is provided with many cilia forming numerous tufts along the blepharoplast. The spermatozoid is surrounded by a cytoplasmic film through which the cilia protrude. The pollen tubes bore their way through the nucellar tissue into the large archegonial chamber into which the archegonia open. Only two sperms are formed in the cycads, except Microcycas, where there may be 16 to 22. In Ceratozamia, exceptionally, four may be formed. In Microcycas they are formed in pairs, developed from a series of body cells cut off from the stalk cell.

The development of the female gametophyte keeps pace with that of the male, and by the time the sperms are fully developed the archegonia are ready for fertilization and open into the archegonial chamber. The free end of the pollen tube, containing the sperms, becomes greatly distended with fluid and finally bursts, discharging the fluid contents, including the two spermatozoids, into the archegonial chamber. The ciliated spermatozoids are thus able to reach the open archegonium and penetrate the large egg. The blepharoplast is detached from the sperm nucleus, which then fuses with that of the egg.

The embryo.—The earliest stages of the embryo have been studied by Chamberlain in

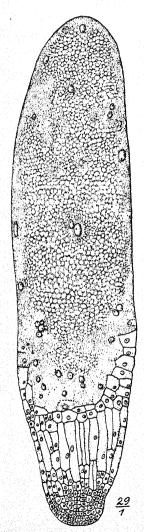


Fig. 258.—Embryo of Zamia floridana (Pilger, after Chamberlain).

Stangeria and Dioon. Unlike the pteridophytes, the early divisions of the nucleus of the zygote are not accompanied by the formation of cell walls, but the embryo for a long time has only free nuclei embedded in the cytoplasm, very much like the early development of the gametophyte. The divisions of the nuclei are simultaneous and the number of free nuclei may reach (theoretically) 512 to 1024. However, the later divisions are not so regular. In Stangeria there is sometimes a distinct polarity, the free nuclei being divided into two groups. The lowest number of free nuclei recorded is in Bowenia, where Lawson reports 64.

Following the free nuclear stage there is the formation of cell walls resulting in an oval cell mass, the "proembryo." In Cycas there is a large central vacuole in the young proembryo, but Chamberlain states that in Zamia, Stangeria, and Dioon the cytoplasm completely fills the proembryo. In Stangeria and Dioon cell formation begins at the base and proceeds upward. There is a good deal of variation in the completeness of the cell division, and the differentiation of the embryo is a very slow process. Some of the cells at the base of the proembryo become elongated and develop into the very much elongated and twisted suspensor, at the end of which the embryo proper is borne. All of the archegonia may develop embryos; but only one comes to maturity, and when the latter reaches a

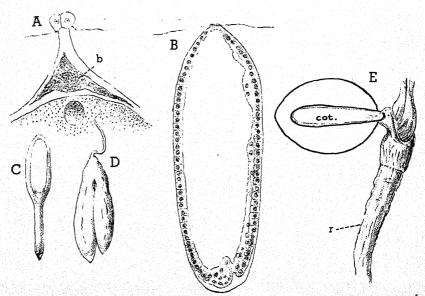


Fig. 259.—A, apex of archegonium in Cycas revoluta; b, canal cell; B, fertilized egg of C, circinalis, showing early stage of embryo; C, D, older embryos; in D, the two cotyledons and suspensor; E, germinating seed of Cycas circinalis; cot, cotyledon; r, root (A, after Ikeno; B-E, after Treub).

fairly advanced stage its suspensor is not a simple structure but includes the suspensors of the abortive embryos as well. The embryo develops two cotyledons and suggests that of the dicotyledons.

In the ripe seed the thick fleshy pulp derived from the outer integument is often bright-colored. Below it is the very hard shell derived from the middle layer of the integument. The inner layer of the integument becomes disintegrated. The cylindrical embryo lies in the axis of the seed, surrounded by the gametophytic tissue, endosperm. The embryo has two large cotyledons, which are free for about four-fifths of their length but have their bases united into a short tubular sheath enclosing the stem apex and young leaves. One of the cotyledons is slightly smaller than the other and in *Ceratozamia* one is almost completely wanting. In *Encephalartos* three cotyledons have been reported. The hypocotyl is very short and the root apex is protected by a hard covering, the coleorhiza, which breaks through the shell of the seed and is penetrated by the elongated root. The first and second leaves are placed at right angles to the plane of the cotyledons, but as new leaves are formed the arrangement gradually develops the spiral character found in the older sporophyte.

A very complete study of the anatomy of the embryo in the ripe seed of *Dioon edule* has been made by Tiessen, but between this stage and the proembryo there is little information and it is not clear just what are the relations to each other of the organs of the embryo in the intermediate

stages.

The great development of the cotyledons and the very rudimentary character of the stem apex suggest that the vascular plate is not a cauline structure but is formed by the union of the cotyledonary traces and that in the cycads, as in the Marattiaceae, no primary cauline stele is present. In the Marattiaceae the bundle of the cotyledon is continuous with that of the root and forms a single axial stele, no vascular tissue being formed in the very rudimentary stem. A comparison of earlier stages in the embryo of the cycads with those in Marattiaceae would be of interest. According to Chamberlain, Matte has expressed much the same idea.

Germination.—With the beginning of germination the base of the embryo elongates, pushing the coleorhiza through the micropyle and protecting the root, which soon penetrates the coleorhiza and pushes downward, becoming a stout taproot penetrating deep into the ground. Only the base of the cotyledons projects from the seed coat, the greater part remaining embedded in the endosperm, which is gradually used up. After several weeks—or sometimes longer—the first leaf emerges, between the cotyledons. The second leaf may not appear for a year or more, and the formation of new leaves is very slow. The first leaves sometimes are imperfectly developed and remain as thick scales or bracts.

Hybrids.—Experiments in crossing different species of cycads have been made successfully. Chamberlain records some important investigations made at the University of Chicago, where he has assembled a notable collection of cycads. As examples he cites successful crossing of species of Zamia, and from the resulting seeds he raised plants which bore cones, in one case within six years. These hybrids when crossed produced seeds from which plants were successfully grown. Still more remarkable was the successful crossing of two genera, Ceratozamia Mexicana and Zamia monticola.

ORDER BENNETTITALES

From the Upper Triassic, and especially throughout the Jurassic the Bennettitales were perhaps the most important elements in the Mesozoic floras. They reached their culmination in the Lower Cretaceous, and ap-

parently none of them survived beyond the Cretaceous.

The study of these fossils until the last decade of the nineteenth century had been made on European material; and in Britain, especially, great advances were made in determining the structures of petrified specimens of the reproductive parts. In 1894 Professor Lester F. Ward published several papers on fossil cycadean trunks from Maryland and from the Black Hills of South Dakota and Wyoming. These were so perfectly petrified that sections could be made showing the details of structure of both the vegetative and the reproductive organs. The abundance of material from the Black Hills region and its extraordinarily perfect preservation made this probably one of the most important discoveries that had ever been made. The results of the studies of this material by Dr. Ward, and especially the further investigations of Professor G. R. Wieland, were by far the most important contributions to the structure of the "floral" structures that have been made. The tissues of the cones were perfectly preserved and did much to make clear the structure and arrangement of the sporophylls and also to throw light on some disputed points in the structure of other forms. Dr. Wieland made repeated collections in the original location, which has recently been set aside as a national reserve. Another extraordinarily rich field was discovered by Wieland in Mexico in the state of Oaxaca. This was much older and was very rich in cycadean fossils. This formation was of Early Jurassic (Lias) age, while the Rocky Mountain fossils were Cretaceous. The discovery of the abundant cycadean fossils in Mexico is interesting, as Mexico is today one of the two chief centers of the existing cycads.

The cycadeoids of the Black Hills region are the latest and most specialized of the Bennettitales; and their structure, both vegetative and reproductive, is so perfectly known that they explain much of the fundamental

structure of the other members of the order. With the discovery of earlier and simpler genera—Williamsonia, Wielandiella, and others—it is clear that the Bennettitales were far more plastic than the Cycadales. While often closely resembling the latter in general habit, of both stem and foliage, and also in their anatomical details, many of them had much more slender stems, in all of them the strobilus was much more specialized, and in many cases, at least, the strobili were bisporangiate. It is mainly on the great difference in the structure of the sporophylls between the Cycadales and Bennettitales that the latter have been placed in a special order.

The trunk in *Cycadeoidea*, the most highly developed of the order, is much like that of the living cycads. The pith and the cortex are extensive and the characteristic mucilage ducts are present and in most respects are much like those of the Marattiales and the fossil Medulloseae, to which both Cycadales and Bennettitales are almost certainly allied.

The best known of the Bennettitales are species of Cycadeoidea. Wieland's remarkable investigations on a number of the American species have afforded by far the most complete account of the details of structure, and this work has been the stimulus to the study of other members of the order outside of America. The strobilus of a European species was first named Bennettites by Carruthers but was later discovered to be the cone belonging to a cycadean trunk which had been described as Cycadeoidea, and Wieland accepted this generic name for the American species.

Most species of Cycadeoidea have short stout trunks completely covered with the old leaf bases and are not distinguishable from similar trunks of some living Cycadaceae. The pinnate leaves also form a crown at the apex of the trunk, and the young leaves show the same circinate vernation found in Cycas. The structure of the leaves is not essentially different from that of the living cycads; and Wieland, speaking of Cycadeoidea ingens, says that leaves might readily be taken for those of Encephalartos or Macrozamia. Some of these isolated leaves of cycadeoids have been described under such names as Zamites, Dioonites, etc., from their resemblance to the leaves of living cycads.

The most fundamental differences between the cycadeoids and the Cycadaceae are in the character of the strobilus. In most cycads the strobilus is formed directly from the apex of the main axis and a secondary apical meristem forms at the base of the cone. In Cycadeoidea there are very numerous small strobili borne on short lateral branches and crowded between the old leaf bases. There may be several hundred of these strobili, and Wieland suggests that this phase marks the end of the life cycle in the individual. These strobili, in most cases at least, bear both ovules and pollen sacs.

The apical region is a conical body, or receptacle, upon which are

borne closely set, slender bodies (sporophylls?) each having at its tip a single ovule. The condition is more like that in some of the pteridosperms than like the Cycadaceae, and perhaps the slender pedicel might better be denominated a sporangiophore. Between the sporangiaphores are sterile filaments, with expanded tips which arch over the ovules, leaving only a narrow pore into which the micropyle opens.

Below the ovular receptacle there was a whorl of pinnate microsporangial sporophylls, looking like fern leaves and joined at the base. The numerous pollen sacs are borne in two rows on the slender pinnae. These pollen sacs were synangia, very much like the synangia of *Marattia* or *Danaea*. Surrounding this bisporangiate strobilus were numerous linear protective bracts.

The structure of the ovule is much like that of the cycads or some pteridosperms. There is a single integument, with a thick, fleshy outer

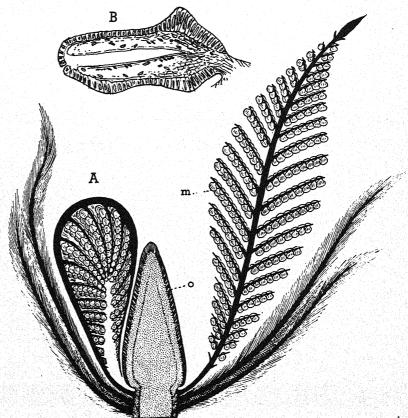


Fig. 260.—Cycadevidea dacotensis, schematic section of the "inflorescence"; o, ovules; m, microsporic synangia ("anthers"); B, section of a synangium (after Wieland).

layer and an inner, stony one. The cortical tissue of the pedicel (sporangiophore?) develops a cupule enclosing the ovule and forming a thin fibrous husk about the ripe seed. The embryo is dicotyledonous and almost completely fills the embryo sac, thus differing from the living cycads, where the embryo is embedded in the abundant endosperm.

Microsporangium.—The pollen sacs are united into an oval synangium; the whole perhaps might be called an anther. The outer wall of the synangium is composed of thick-walled palisade cells, and the inner tissue surrounding the loculi is made up of smaller, thin-walled tissue. There are two rows of loculi, as in Marattia, and the dehiscence of the synangium seems to have been much the same; i.e., the ripe synangium splits into two valves, forming a median cleft into which the individual loculi open. The pollen spores are small but are larger than in the living cycads. Wieland found evidences of cell formation within the pollen spore, recalling Cordaites. Whether or not the cells within the pollen spores are spermatocytes is not clear. It may be assumed that fertilization was by active spermatozoids, but whether or not a pollen tube was developed is not known.

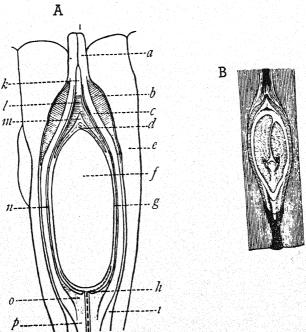


Fig. 261.—A, longitudinal section of a seed of Bennettites (Cycadeoidea) Morieri; m, pollen chamber; f, embryo sac; a, micropylar tube; B, section of seed of Cycadeoidea Gibsoniana (A, after Wieland; B, Kräusel, after Solms-Laubach).

The Cycadeoideae probably were the most recent and most specialized members of the order. It is thought that they represent a relatively late offshoot of the main line of development of the Bennettitales, which thus culminated during the Cretaceous era.

WILLIAMSONIOIDEAE

In the Upper Triassic, and especially during the whole of the Jurassic, many fossils are found which obviously belong to the Bennettitales but are of simpler structure as regards the inflorescence, compared with the cycadeoids. Most of these Jurassic types have been referred to the suborder Williamsonioideae and seem to have formed the major part of the Jurassic cycadophytes. "Of all post Palaeozoic gymnosperms, the type represented by Williamsonia is the most generalized and plastic and capable of floral variation."

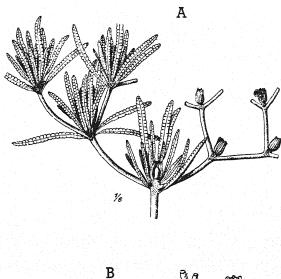
The first of the Williamsonioideae to be critically studied was Williamsonia gigas, from the Middle Jurassic of the Yorkshire coast. It was originally described as Zamites gigas. It resembled a slender-stemmed cycad, having a crown of large, Zamia-like leaves, and was assumed to be a true cycad. The reproductive structures, the strobili, are lateral like those of the Cycadeoideae; but the shoots on which they are borne are much longer and the strobili are of greater size. Scott compares them in size and general appearance to an artichoke. These strobili were not petrifactions, and the internal structures could not be studied. Other species of Williamsonia with petrified strobili show a structure much like Cycadeoidea; but they had only ovules, and it is probable that the microsporangia were not produced by the same strobilus. Microsporangial sporophylls much like those in Cycadeoidea have been found, but never in connection with the ovular strobilus. The sporophylls like those in Cycadeoidea are united at the base, but much more completely, as they form a cup-shaped structure, the "staminal disc," with the ends of the sporophylls forming a fringe about the margin. In some species, e.g., W. spectabilis, the free portion is conspicuously pinnate, as in Cycadeoidea, and the synangia are borne on the pinnae; in others, e.g., W. Whitbyensis, the sporophylls are entire and the synangia are in two rows along the inner face.

The strobilus in Williamsonia may be invested with special bracts, or these may be absent. Usually associated with Williamsonia are two very remarkable fossils which differ greatly in habit from the other Bennettitales. These are Wielandiella augustifolia and Williamsoniella coronata. Kräusel, in his treatment of these in the Natürlichen Pflanzenfamilien, proposes a special suborder—Wielandielloideae—for these genera.

They have slender, forking stems very different from those of the typi-

¹ Wieland, American Fossil Cycads, 2: 177.

cal cycadophytes, and the simple leaves are small and narrow, either in clusters at the forks (Wielandiella) or scattered on the shoot (Williamsoniella). The strobili are small. In Wielandiella they are sessile, and are surrounded by a tuft of narrow leaves; in Williamsoniella the "flower" has a conspicuous pedicel and the sporophylls are entirely exposed. Indeed the superficial resemblance to a simple angiospermous flower is quite remarkable, especially in Williamsoniella. Wielandiella is first met with in



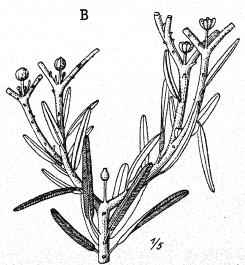


Fig. 262.—A, Wielandiella angustifolia; B, Williamsoniella coronata (restorations, Kräusel; A, after Nathorst; B, after Hamshaw-Thomas).

the Upper Triassic (Rhaetic). Williamsonia, at present, is known only from the Jurassic of Yorkshire, where it was discovered by Professor H. Hamshaw Thomas.

In Williamsoniella the forking branches are about a centimeter in diameter. Associated with the stems were narrow leaves, which have been described as a fern, "Taeniopteris." The "flower" was borne at the end of a slender branch or peduncle 3-6 centimeters long. The apex of the shoot formed a conical receptacle, having numerous ovules mingled with "interseminal scales," like those of the other Bennettitales. The apex of the receptacle was sterile and formed into a curious "corona." Around the base of the receptacle was a circle of free microsporophylls or stamens. These had an elevated median ridge with three synangia on each side.

Wielandiella.—The stem of Wielandiella seldom exceeded 1.5 centimeters in diameter. The branching, a false dichotomy, resembles the leaf of some species of Gleichenia. The sessile strobili, which are situated in the forks of the shoot, are completely enveloped by numerous narrow bracts. It is not certain whether the strobili were monosporangiate or bisporangiate.

ORIGIN AND INTERRELATIONSHIPS OF THE CYCADOPHYTA

The many similar structural details in the living Cycadaceae and numerous Mesozoic fossil stems and leaves make it certain that there is a genetic connection between Cycadales and Bennettitales. As is so often the case, the surviving cycadophytes represent the simpler and presum-

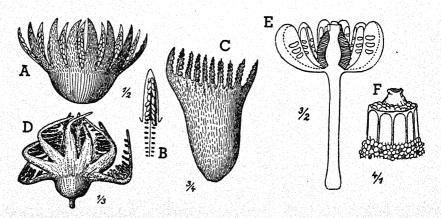


Fig. 263.—Flowers of Williamsoniaceae. A, B, Williamsonia whitbeyensis; C, W. mexicana; D, W. spectabilis; E, Williamsoniella coronata, schematic figure of a "flower"; F, upper part of the "pistil" (A-D, Kräusel, after Wieland; E, F, after Hamshaw-Thomas).

ably older types which have survived, while the very specialized Bennettitales were completely superseded by the angiosperms.

That the cycadophytes are descended from fern-like ancestors allied to the existing Marattiaceae is extremely probable; but this implies a derivation not from any existing forms but from a much more extensive Palaeozoic fern-pteridosperm complex to which the Marattiaceae were related.

Wieland, whose knowledge of the fossil cycadophytes is unsurpassed, has called attention to the many points of structure common to the Cycadales and the Bennettitales and to the true ferns, especially the Marattiales. There are two distinct types of sporangium in the latter: individual sporangia, e.g., Angiopteris; and solid synangia, e.g., Marattia and Danaea. He concludes that the Cycadales are derived from marattiaceous ancestors with sporangia of the Angiopteris type, while the Bennettitales were derived from forms with solid synangia, like Marattia.

Wieland states further: "For the sake of specific clearness it may be added that we may well conceive of two closely related Marattiacean genera, one with sori of the Angiopteris type, and the other with synangia like Marattia, undergoing a series of parallel changes not completely chronologic and giving respective and separate origin to the Cycadeoidea and the Cycadaceae. In such a case, the main point is that this pair of hypothetical ancestral genera must have retained complementary family relationships after the assumption of the primitive cycadaceous form. But of small finer gradations of homoplasy we can have but a vague and nebulous idea, and it must be pleaded that it affords a clear conception of morphologic and biologic relationships to regard the ancestors of the Cycadeoideae as integrally cycadean, or perchance Cycadofilicinean rather than simply Marattiaceous."

The Cycadaceae have retained their primitive fern-like habit, with massive trunk and pinnate leaves. In Cycas the megasporophylls are obviously foliaceous, and this is also evident in the other genera, although they are crowded into a strobilus. The filicinean relationship is also emphasized by the motile multiciliate sperms. The Williamsonia type has much the same habit as the Cycadaceae, but its strobilus is more specialized.

In the Cycadeoideae the very elaborate "inflorescence" is the culminating effort of the group in its latest development, in the Cretaceous, perhaps coeval with some of the ancestral angiosperms, which soon become dominant. While the arrangement of the sporophylls in *Cycadeoidea* is strikingly like that in the ranalean angiosperms, and they have been sug-

¹ Wieland, op. cit., 1: 240.

gested as possible ancestors of the latter, the highly specialized character of the cycadeoidean "inflorescence," especially the microsporophylls, would seem to point to these as the end of a side line which became extinct in the Cretaceous. It is the earlier and simpler Williamsonia types which were dominant during the Jurassic and Late Triassic; and some of these may have been the progenitors of the "Proangiosperms," as well as of the Cretaceous cycadeoids.

It is difficult to connect Williamsoniella and Wielandiella with either the Cycadales or the Williamsonia type, and it is possible that these may have been derived directly from some of the pteridosperms, where the forking habit of the slender stems is characteristic. However, the structure of the sporophylls and the synangia indicates a relationship with the Bennettitales.

The striking similarity in the arrangement of the floral organs between the Cycadeoideae and some of the ranalean angiosperms has led to considerable speculation as to the possibility of such types as the Magnoliaceae being derived from the Bennettitales. Even more flower-like is the strobilus of Williamsoniella; and while these are doubtless cases of homoplasy, it is quite likely also that the "Proangiosperms" originated from forms distantly related to these and it is quite possible that in the immense complex of cycadean plants which dominated the Mesozoic floras the ancestors of some of the angiosperms had their origin. This does not mean that all the angiosperms had a common ancestor. Possibly, we may say, the "Proangiosperms" were Bennettitales.

While it is customary to consider the cycadophytes as "gymnosperms," it might be suggested that the massive investment of the ovule in the Cycadaceae is possibly not a single integument but that the thick outer portion might be the beginning of a carpellary structure fused with the integument—a sort of pericarp, so to speak. This might also be applied to the "cupule" found in some cycadophytes.

CHAPTER XX

GYMNOSPERMS—CORDAITALES, GINKGOALES

CORDAITALES

Among the most characteristic fossils of the later Carboniferous and Permian are remains of trees, sometimes of large size, which recall the living conifers but differ from them in important respects such that their exact relationship with the living gymnosperms is not at all clear. Many of these fossils have been assigned to a special order, Cordaitales, of which the best known is *Cordaites*. Many examples of petrified wood and leaves and also shoots bearing pollen sacs and ovules have been found, as well as seeds, so that the anatomical characters are fairly well known.

Some species of Cordaites were tall trees with trunks 20 to 30 meters high. The trunk divided at the summit into a spreading crown of branches bearing large lanceolate leaves with parallel venation, like that of many monocotyledons, e.g., Yucca, Cordyline, or some bamboos. Among the living gymnosperms, the Kauri pines (Agathis) probably most nearly resemble Cordaites in habit. Agathis australis, the Kauri pine of New Zealand, has a very massive cylindrical bole, dividing at the top into several widespreading main branches, differing greatly in appearance from the typical conifers. The leaves of Agathis are also much like those of Cordaites in both shape and venation, although much smaller.

The stem.—The anatomy of the stem in Cordaites is very much like that in the living conifers, especially the Araucariaceae. It differs mainly in the greater size of the pith, in which it is more like the cycads. The pith in longitudinal section shows numerous diaphragms instead of the solid pith found in other gymnosperms.

The solid woody cylinder has the protoxylems next to the pith, and there is developed a thick zone of primary wood composed of large spiral and scalariform tracheids. These finally merge into the secondary wood, the tracheids of which have crowded bordered pits like those in the conifers, especially the Araucariaceae; hence much of the cordaitean fossil wood has been described as "Araucarioxylon." Traversing the wood are narrow medullary rays like those of coniferous wood. In typical Cordaites there is no evidence of seasonal growth rings; but in supposed cordaitean wood from Siberia and Antarctica, according to Seward, definite growth rings have been found. In the thick cortex "secretory sacs" occur, sug-

gesting the mucilage ducts characteristic of the cycads and found also in Ginkgo.

The leaves.—The large leaves of Cordaites are somewhat crowded and are spirally placed upon the smaller terminal branches. When the leaf is shed it leaves a conspicuous scar with a cushion below it. The surface of the shoot from which the leaves have fallen resembles that of the living pines and firs.

The petrified leaves of Cordaites are abundant and their structure is well preserved. Scott compares their structure with that of a single pinna of the compound Cycas leaf, or the leaf of Agathis. The structure, on the whole, is much like that of the typical leaf of a fern or flowering plant. There may be a well-marked palisade layer between the upper epidermis and the lower mesophyll, which is spongy, with intercellular spaces communicating with the stomata of the lower epidermis. The vascular bundles of the veins are concentric; but the xylem is divided into two parts, the upper larger than the lower, with small spiral tracheids between. According to Scott, "We have in these cases the collateral, mesarch structure, characteristic of cycadean leaves."

The roots.—The root structure of Cordaites is much like that of the living conifers. The larger roots may be diarch, or there may be several

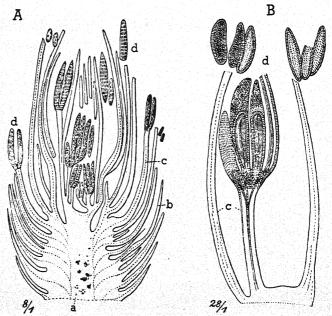


Fig. 264.—A, longitudinal section of male inflorescence of Cordaianthus Penzoni; b, sterile bracts; c, sporangiophore ("stamen"); B, sporangiophores (Kräusel, after Renault).

protoxylems. The secondary growth of the roots is like that of the stem, and in the cortex there is periderm, which contributes to the growth of the cortical tissues.

Sporangia.—While the anatomical details of the tissues of the Cordaitales are readily comparable with those of the existing conifers, and to some extent with the cycads, the reproductive organs are very different from those of any other gymnosperms and it is difficult to make a comparison. Our knowledge of the structure of the sporangia is mainly due to Renault's investigations of petrified material of the inflorescences of several species of Cordaianthus.

The sporangia (pollen sacs, ovules) in *Cordaites* were borne upon slender leafless branches attached to the shoot above the insertion of the leaves. These fertile branches are usually found detached and were first described under the name *Antholithus*. They are now usually referred to as "Cordaianthus." Attached to these branches are small cones, or catkins, composed of closely imbricated scales or bracts, which in most cases completely conceal the sporangia, so that externally the two sorts of cones are not always distinguishable.

The cone bearing the microsporangia or pollen sacs has numerous bracts, between which are slender sporangiophores, having at the apex several elongated pollen sacs. The sporangiophore has an axial vascular bundle. The sporangiophore with the attached pollen sacs has sometimes

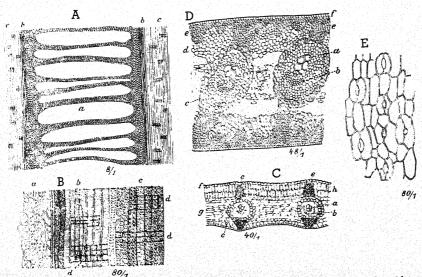


Fig. 265.—A, section of young branch of Cordaites, showing diaphragms in the pith; B, section of wood; C, cross section of leaf of Cordaites sp.; D, similar section of leaf of C. lingulatus; E, lower epidermis of leaf of C. crassus (all figures from Kräusel, after Renault).

been called a stamen but differs from the stamens of the higher seed plants in having the pollen sacs separate instead of united into a synangium. In some cases the structure of the large oval microspores can be distinguished. They were multicellular, containing a group of small cells, possibly representing an antheridium containing several spermatocytes. It is probable that, like *Ginkgo* and the cycads, there were active ciliated spermatozoids.

Among the living gymnosperms, Ginkgo most nearly resembles Cordaites in the character of the sporangiophore. The pollen sacs of Ginkgo, usually in pairs and sessile, are borne also on an elongated sporangiophore. The sporangiophore has also been compared with that of Ephedra of the

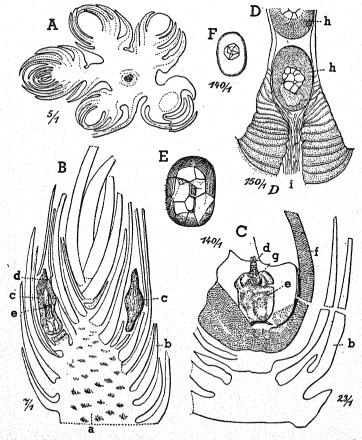


Fig. 266.—A, cross section of axis of Cordaianthus subglomeratus; B, longitudinal section of female inflorescence of C. Williamsoni; c, ovules; C, section of an ovule; d, micropyle; g, pollen chamber; D, upper part of nucellus, with two pollen grains; E, F, pollen spores, showing multicellular contents (all figures from Kräusel, after Renault).

Gnetales; but Scott thinks the comparison with Ginkgo is more plausible, especially as practically nothing is known of fossil Gnetales.

The cones which bear the ovules have the bracts arranged like those of the microsporangial ones; but most of the bracts are sterile and the number of ovules is small, even in some cases reduced to a single terminal one. They are situated in the axils of the fertile bracts and have a short pedicel. The somewhat flattened ovules have a single thick integument, the inner portion of which becomes hard as the ovule develops. A pollen chamber is formed at the top of the nucellus like that in the pteridosperms and cycads; but no evidence of a pollen tube has been observed, and it may be that the spermatozoids were discharged directly into the pollen chamber and thus reached the archegonium. Various fossil seeds, probably belonging to the Cordaitales, have been described. One of the best-known is Cardiocarpus.

Relationships of the Cordaitales.—Like the pteridosperms, the Cordaitales have left no immediate descendants, and they apparently became extinct at the close of the Palaeozoic era. While they show marked resemblances in their structure to three existing orders of gymnosperms—Ginkgoales, Cycadales, and Coniferales—there is little reason to believe that any of these are their direct descendants. There are also indications of relationship with pteridosperms, but just how close the relationship is not at all clear.

Professor Scott in his summary of the affinities of the order (Studies in Fossil Botany, 3d ed., Vol. 2, p. 311) says: "In their vegetative characters the Cordaiteae hold the balance very evenly between Cycads and Conifers, while at the same time showing much that is peculiar to themselves. The structure of the stem and root is on the whole very near that of the Coniferae; the secondary wood would by itself rouse no suspicion that we had anything but an Araucarian Conifer before us. The large size of the pith in the stem, however, is unlike anything known in Coniferae, and rather suggestive of a Cycad, though in its peculair discoid structure the pith of some Cordaiteae is quite different from that of the Cycads.

"The double leaf-trace is a striking point of agreement with Ginkgo on the one hand and certain of the Pteridosperms on the other."

As might be expected, the most marked similarities are with those gymnosperms which are generally recognized as the most ancient types, viz., Araucariaceae, Cycadaceae, and Ginkgo. In general habit Agathis suggests Cordaites, with which it agrees also in the shape and venation of the leaves. The arboreal habit of Ginkgo is also consistent with a relationship with Cordaites; and while the leaves differ in form, their dichotomous fern-like venation is similar. Ginkgo also seems most nearly among living gymnosperms to resemble Cordaites in its reproduction.

However, the data regarding the development of *Cordaites* are still too fragmentary to make possible any but tentative theories as to their systematic position.

GINKGOALES

The second order of living gymnosperms, the Ginkgoales, has but a single species, $Ginkgo\ biloba$, sometimes called the "maiden-hair tree" on account of the leaves which in form and venation are much like the leaflets of some species of Adiantum. Ginkgo has been called a "living fossil," since it has existed with little change from the Jurassic to the present day and is not known to exist in a wild state. It has long been planted about the temples in China and Japan and has been introduced into the United States, where, especially in the Atlantic states, it finds a congenial home. Until the discovery by the Japanese botanist Hirase, in 1896, that multiciliate spermatozoids occur in Ginkgo as in the cycads, the latter was placed in the Coniferales; but it is now assigned to a special order, Ginkgoales.

The geological history of Ginkgo is comparable with that of the cyca-

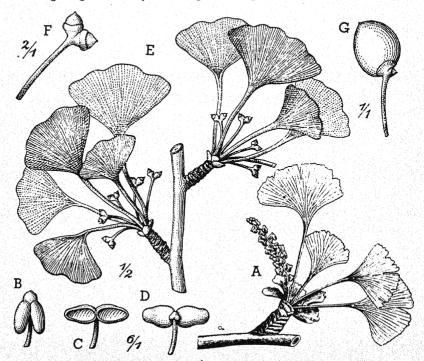


Fig. 267.—A, shoot of Ginkgo biloba, bearing male strobilus; B-D, three views of a sporangiophore (stamen) with two pollen sacs; E, branches bearing ovular sporangiophores; F, sporangiophore with two ovules; G, seed (after Pilger).

dophytes, and like the latter, during the Jurassic, they were worldwide in distribution. The Ginkgoales can be traced back to the Palaeozoic (Permian), but like the cycadophytes they culminated during the Jurassic, in which leaves and flowers have been found scarcely distinguishable from those of the living species.

The earlier fossil leaves are more deeply lobed than those of the living Ginkgo, often having very narrow, dichotomously divided segments. These early fossils are generally referred to a second genus, Baiera, but it is not always possible to distinguish between the Baiera type and Ginkgo.

There are many leaf impressions from the coal measures much like Ginkgo, but it is quite as likely that these belong to true ferns or pteridosperms. The genus Ginkgo may be traced from the Jurassic to the present.

Ginkgo biloba is a large tree, sometimes 30 meters or more in height, with a trunk diameter of a meter or more. When young it has a pyramidal form with a central trunk bearing numerous lateral branches, like most conifers and also like many angiospermous trees. Indeed the young Ginkgo is suggestive of a young birch or aspen poplar. In the old trees there is a much-branched, spreading crown. The broad deciduous leaves are very different in appearance from the needles of the pines and firs and similar conifers, which with the exception of the larch and the bald cypress (Taxodium) are evergreen. There are two sorts of shoots: the elongated terminal shoots with scattered leaves, and numerous short lateral branches or spurs, with crowded tufts of leaves at their summits. These might be compared with the short, leaf-bearing shoots of a larch or a pine.

The leaves of Ginkgo have a slender petiole and broad, fan-shaped lamina with a more or less lobed margin and usually a median cleft so that the leaf is bilobed. Sometimes the lobes may be further divided, recalling Baiera. There are two collateral vascular bundles in the petiole, each of which divides at the base of the lamina into two branches which undergo repeated dichotomy, resulting in a type of venation like that in many ferns, e.g., Adiantum, Trichomanes, and Anemia. A definite scar marks the position of a fallen leaf. The very characteristic form and venation of the leaf makes the identification of fossils, as least in the Mesozoic formations, very easy. There is no definite palisade tissue—stomata are developed on the lower side only.

ANATOMY OF THE STEM

The structure of the stem in *Ginkgo* is much like that of the typical conifers. There is a single permanent layer of cambium from which a cylinder of secondary wood is developed, instead of the successive cambiums found in the cycads. The secondary wood forms a massive solid cylinder making up the bulk of the stem. The pith is small, and the cortical region is

relatively less developed than in the cycads and structurally is much like that of such conifers as Pinus or Abies. Annual growth rings are formed and in general the structure is very much like that of the typical conifers. According to Chamberlain the protoxylem is composed exclusively of spiral tracheids, which are most numerous in the short spur shoots. The secondary wood is composed of tracheids with bordered pits like those of typical conifers. The medullary rays are less developed than in the conifers. Secretory cells and cavities, comparable to the mucilage ducts of the cycads, or the resin ducts of the conifers are abundantly developed. Unlike the latter, however, they are formed from groups of secretory cells which fuse into a single mass but do not form elongated ducts like those of the conifers. Differing from the latter, they are "lysigenous," i.e., formed by coalescence of a mass of cells—whereas in the conifers the resin ducts are elongated intercellular spaces into which resin is discharged. Chamberlain speaks of "mucilage" in connection with Ginkgo, but Pilger refers to "Harz-gänge," i.e., resin ducts differing from those of the conifers in being lysigenous. Tannin cells are also present.

In the dwarf shoots the pith and cortex are relatively larger and the structure more suggestive of the Cycadales. The root of the young sporophyte is usually diarch and the mature root, like the stem, shows annual rings and tracheids with bordered pits.

Like the cycads, Ginkgo is dioecious, with pollen sacs in pairs attached to a knob at the end of a slender stalk or pedicel. This might perhaps be called a sporangiophore, and the whole structure is possibly comparable to the stamen of the higher flowering plants. The sporangiophore bearing the two pendent microsporangia recalls the sporangiophore of Equisetum. Pilger states that there may be three or even four pollen sacs. The "stamens" form a catkin-like inflorescence, borne at the apex of the dwarf shoots. This inflorescence has been compared with that of Cordaites and Jeffrey compares it with the male cone of the Pinaceae. In neither case is the similarity very marked.

The pollen spores are much like those of the cycads, and at the time of pollination consist of three cells, viz., prothallial cell, generative cell, and tube cell. There are also the remains of a primary prothallial cell. In the cycads the primary prothallial cell remains intact.

The megasporangia (ovules) are also usually in pairs at the apex of a slender pedicel the nature of which is not entirely clear but which might also perhaps be considered a sporangiophore. Like the male catkins, the ovulate sporangiophores are borne on the dwarf shoots. Each ovule has at its base a collar, which recalls the "cupule" of some pteridosperms and was compared by Strasburger to the "aril" of Taxus. The morphological character of the latter, however, is not certain. It may perhaps represent

a second integument—or even the beginning of a carpellary structure. The development of embryo sac, pollen chamber, etc., is very much as in the cycads.

There are many free nuclei in the young embryo sac before any cell walls are developed, and the further development of gametophyte and archegonium is very much as in Cycas (for details, see Coulter and Chamberlain, Gymnosperms, pp. 203–205). The most notable difference is the presence of a definite ventral canal cell in Ginkgo, while in Cycas no cell wall separates the canal cell nucleus from that of the egg.

Pollination and fertilization in *Ginkgo* were first investigated by Hirase, whose studies were made in Tokyo. The pollen was shed in April and early May and deposited on the ovules, where it germinates and the pollen tubes penetrate the tissue of the nucellus and finally reach the pollen chamber into which the spermatozoids are discharged, as they are in the cycads. The development of spermatozoids and pollen tube is essentially the same as in the cycads, but the spermatozoids are only about half the diameter of those of *Cycas* and the blepharoplast is less developed. From the time the pollen is shed to the discharge of the spermatozoids is about four months.

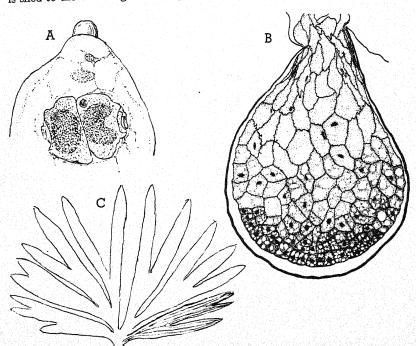


Fig. 268.—A, pollen tube of Ginkgo, containing two large spermatozoids; B, embryo of Ginkgo; C, leaf of Baiera gracilis, a fossil related to Ginkgo (A, from Pilger, after Hirase; B, after Lyon; C, from Chamberlain, after Renault).

THE EMBRYO

The early development of the embryo may be compared with that of the cycads, especially *Dioon*. The nucleus of the fertilized egg divides repeatedly until there are approximately 256 free nuclei distributed through the cytoplasm of the zygote. This "proembryo" then becomes transformed into an oval mass of undifferentiated cellular tissue, cell walls forming between the free nuclei. The basal portion of the proembryo next develops an active small-celled meristem, while in the upper (micropylar) region the cells remain undivided but increase somewhat in size, sometimes pushing through the neck of the archegonium. The undifferentiated cells of the apical region may be considered as a sort of suspensor, but there is not developed the greatly elongated and conspicuous suspensor found in the cycads.

From the basal meristem a conical body is developed which pushes into the adjacent prothallial tissue (endosperm), and this conical body becomes the apex of the embryo sporophyte. Two cotyledons are usually developed, but sometimes there are three.

The ripe seed of Ginkgo is much like that of the cycads. It has the same thick integument, the outer part becoming fleshy, so that the ripe seed resembles a stone fruit like a plum or cherry. The middle layer of the integument has the same stony texture as the corresponding layer in Cycas, and within this is the third thin layer. The embryo, which resembles in form that of the cycads, is relatively much smaller, with a corresponding increase in the amount of endosperm.

When the seed germinates, the greater part of the cotyledon remains within the seed and acts as a haustorium to supply food to the young sporophyte. The bases of the cotyledons, however, elongate and push the apex of the seedling outside the seed coat.

The anatomy of the young seedling is much like that of the cycads but is less fern-like and more like the more specialized Coniferales. Chamberlain states that the primary root is originally tetrarch and is related to the four cotyledonary strands from the transition region. By a fusion of these bundles in pairs, the root becomes diarch or, where there are three cotyledons, triarch.

RELATIONSHIPS

Like the cycads, the Ginkgo type has survived with little change from the Early Mesozoic; and while there are evidences of a derivation of the Ginkgoales from the complex of filicinean types—ferns and pteridosperms—some of the marked similarities between the cycadophytes and the Ginkgoales are probably homoplastic, and the two phyla have remained distinct at least from the Late Palaeozoic.

Among the later conclusions as to the relationships of the Ginkgoales is the theory that the nearest relatives of the order are the fossil Cordaitales. Scott concludes: "On the whole the sum of fossil evidence is of sufficient weight to prove the great antiquity of the family now represented by the Maidenhair tree, which appears to be best regarded as the one surviving member of an ancient stock derived from the same cycle of affinity as the Palaeozoic Cordaiteae, once the dominant type of Gymnosperms."1

Among the existing gymnosperms Ginkgo resembles on the one hand the cycads and on the other the conifers. "The characteristics in common with the Cycads are primitive, shared with the Cycadofilicales and Cordaitales, while the characters in common with the Conifers are distinctly ad-

vanced."2

We may conclude that the Ginkgoales have retained certain primitive characters, such as the active spermatozoids, shared with the cycads but not derived from them; but on the whole their development has followed lines much more like that of the conifers, although here again this trend has gone on quite independently and there is little ground for the assumption of any real genetic relationship between Ginkgoales and Coniferales.

¹ Scott, Fossil Botany, 2: 385.

² Coulter and Chamberlain, Gymnosperms, p. 217.

CHAPTER XXI

GYMNOSPERMS—CONIFERALES

The existing cycads and Ginkgo are evidently relicts of a flora once much more extensive than at present. The Coniferales, on the other hand, although comprising only about four hundred species, play a very important role in the vegetation of the modern world. Over extensive areas, like western North America and parts of Europe and Asia, they constitute the major elements in the forests, sometimes forming extensive stands of a single species, like parts of the redwood belt of northern California and the Douglas fir forests of Oregon and Washington. Their gregarious habit and the excellence of their wood make the great coniferous forests the most important sources of structural timber. The conifers are mostly trees, some of gigantic size, like the redwoods, pines, firs, and spruces of the Pacific coast and the Kauri pines of Australasia. A smaller number, like some species of junipers, are shrubs.

While conifers are found in practically the whole of the North Temperate Zone, they reach their maximum development in the Pacific regions of North America and Asia. The coastal forests of California, Oregon, Washington, British Columbia, and the western slopes of the Sierra Nevada and Cascades mark the climax of the coniferous forests and are the home of the largest of all known trees. In the Southern Hemisphere the conifers are most abundant in the temperate regions of New Zealand, Australia, and

South America. They are less numerous in the tropics.

There is a marked difference between the types of the Northern and Southern hemispheres, most of the genera and even the families being restricted to one or the other. Thus the pine family, Pinaceae, is exclusively northern, and this is true also of the redwood family (Taxodiaceae) and, with a single exception, the yews (Taxaceae). On the other hand the Araucariaceae are almost entirely confined to the Southern Hemisphere, and for the most part this is true of the Podocarpaceae.

The oldest fossil conifers seem to be most nearly related to the Araucariaceae and the Podocarpaceae, both characteristically austral types. It may be that the northern conifers are the modified descendants of these primitive types which have become adapted to the extreme conditions of the continental climates which prevail over much of the northern lands, while the more primitive araucarian and podocarpus types have persisted in the less extreme climates of the Southern Hemisphere.

FOSSIL CONIFERS

Fossils referable to the Coniferales have been found in Permian and possibly in Late Carboniferous formations; but these primitive conifers, some of which occur also in the Triassic, cannot be certainly assigned to any of the existing families, although they show some evidences of possible relationship with them. Like the Cordaitales these earliest conifers were apparently generalized types. Two genera, Walchia and Voltzia, may be cited as showing evidences of a possible relationship with the Araucariaceae, a family now restricted to the South Temperate regions and the adjacent tropics.

While remains of conifers are abundant from the Permian onward, the earlier fossils are mostly impressions of twigs and leaves not sufficiently definite for determination of near relationships. There is good evidence that forms related to the Araucariaceae existed as early as the Triassic and possibly the Permian. From the Jurassic onward the family

was well established and widely distributed.

Some of the early conifers were trees of great size. In the Petrified Forest of Arizona, of Triassic age, are entire trunks of huge trees almost rivaling the Californian redwoods. The wood structure is said to be practically identical with that of the living Araucariaceae, but unfortunately

the foliage and the fructification are unknown.

In the Jurassic, although there are abundant remains of conifers with leaves and branches much like those of living genera, their association with fructifications that can be assigned to living genera can seldom be demonstrated. "Our knowledge of Mesozoic conifers is lamentably incomplete; there are many genera and species represented by pieces of sterile foliage shoots, some bearing long and narrow leaves in two ranks, as in the Yew the redwood tree ; some with crowded and more or less sickle-shaped leaves like those of Araucaria excelsa or Cryptomeria. It is seldom that the fossil twigs bear cones or other reproductive organs well enough preserved to be used as tests of affinity."1

In spite of the difficulty of identifying the Jurassic conifers, it is probable that all of the existing families, or at least their direct ancestors, were

represented.

CLASSIFICATION

The classification of the Coniferales is by no means definitely settled, and many systems have been proposed. One of the most recent, the treatment of the order by Pilger in the second edition of Engler and Prantl's Die Natürlichen Pflanzenfamilien, will be followed here. Pilger recognizes seven families: Taxaceae, Podocarpaceae, Araucariaceae, Cephalotaxaceae, Pinaceae, Taxodiaceae, Cupressaceae.

¹ Seward, Plant-Life through the Ages, p. 364.

GENERAL MORPHOLOGY

The conifers include the largest known trees. The California coast redwood, Sequoia sempervirens, may reach a height of over 350 feet, and S. gigantea attains a diameter of 30 feet at the base of the trunk. The famous cypress of Tule (Taxodium mucronatum) near Oaxaca in Mexico, according to Chamberlain, has a trunk 16 meters in diameter.

All of the conifers branch freely; and, owing to the persistence of the terminal shoot in many of them, the young trees are extremely symmetrical and this condition persists until the trees reach a great height. In such forms the lateral branches are more or less regularly disposed in circles and the tree has a very regular conical outline. Where the terminal shoot is injured one of the branches of the youngest whorl of lateral branches may grow upward and assume the role of the leader.

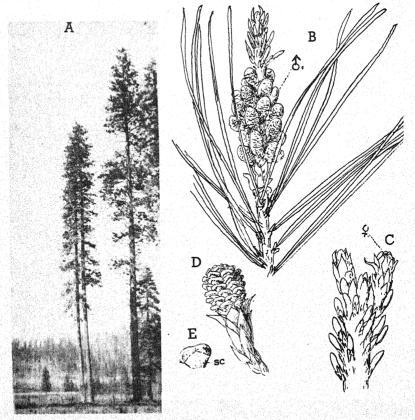


Fig. 269.—A, yellow pine (Pinus ponderosa); B, branch of Pinus Virginiana, with staminale cones, &; C, young ovulate cones, &, of P. virginiana; D, ovulate cone of P. halepensis, single scale with subtending bract, sc.

In old trees the leader is usually lost and a broad spreading crown is formed composed of several main branches. This is common in old specimens of various pines like the Italian stone pine (*Pinus pinea*) and the Californian Digger pine (*P. sabiniana*).

The leaf.—The leaves of the conifers are most commonly slender "needles" like those of the pines and firs, or else short thickened scales as in most of the Cupressaceae, e.g., Cupressus, Thuja. In Agathis, belonging to the Araucariaceae, however, the leaves are broad, recalling the leaves of Cordaites or the leaflets of the cycads. These leaves have numerous veins, which fork at the base of the leaf, while in the Pinaceae and Cupressaceae there is a definite midrib with one or sometimes two vascular bundles. Some of the Podocarpaceae have leaves much like those of the Araucariaceae, and in Sciadopytis and Phyllocladus the leaves are rudimentary and replaced by flattened, leaf-like shoots (phyllocladia).

The leaves may be uniformly distributed on the shoots; or there may be, as in *Ginkgo*, short spur-branches bearing fascicles of leaves. Examples of the latter are *Pinus*, *Cedrus*, and *Larix*.

ANATOMY

The anatomy of the conifers has been the subject of many investigations, and since the woody stems are often very perfectly preserved in fossils this has resulted in somewhat exaggerated importance given to certain structural details as indications of relationship.

In general the stem structure is much alike in all the Coniferales. Among the other gymnosperms, *Ginkgo* is most like the conifers; but both cycads and *Cordaites* show similarities in stem structure, though having the woody tissue less developed and a corresponding increase in the cortex and pith, the latter becoming almost obliterated in the older coniferous stem.

A cross section of the stem of a typical conifer, e.g., *Pinus*, shows a relatively thin cortex and a massive woody cylinder, due to the activity of the persistent cambium. Within the woody cylinder is the pith, which is hardly recognizable in the older trunk.

The vascular bundles of the stem are "endarch"; that is, the formation of the wood is entirely centrifugal. The primary wood, the protoxylem elements, are narrow spiral vessels in contact with the pith; the secondary wood (metaxylem) is composed of radiating series of large tracheids with characteristic bordered pits on their radial walls. At intervals between the rows of tracheids are single rows of smaller cells with protoplasmic contents. These are the medullary rays. The fully developed tracheids have no living contents. A longitudinal section shows that the medullary rays are composed of several rows of cells.

At the outer limit of the woody cylinder is the cambium, the cells of which undergo repeated tangential divisions, the innermost cells gradually becoming transformed into tracheids or adding to the medullary rays. The outer cells of the cambium contribute to the phloem or inner bark. The older phloem contains sieve-tubes, fibers, and elongated parenchyma. The cortex in the young shoot is composed largely of green parenchyma; but later there is formed below the epidermis, a cortical cambium or "phellogen" from which the corky outer bark originates. In both cortex and wood numerous resin ducts are formed. These consist of elongated intercellular spaces or canals filled with resin secreted by the cells surrounding the duct. These resin ducts closely resemble the mucilage ducts of the Cycadales and the Marattiales.

In most conifers definite annual growth rings are formed in the wood; but when there is no marked seasonal interruption of growth, the growth rings are not always clearly marked. In most of the conifers of cold regions the apex of the shoot is protected by closely set, thin scales, forming

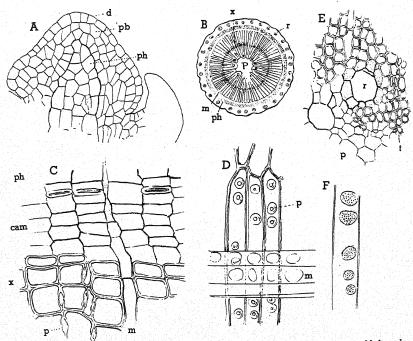


Fig. 270.—A, shoot apex of Sequoia sempervirens; B, section of two-year-old branch of Pinus virginiana; p, pith; x, wood; ph, phloem; m, medullary rays; r, resin ducts; C, section of stem of Taxodium; ph, phloem; cam, cambium; x, tracheids; p, pit in tracheid walls; m, medullary ray; D, tangential section of wood of Pinus radiata, showing bordered pits; E, cross section of inner part of the wood; t, primary tracheids; p, pith; r, resin duct; F, sieve tube of P. sylvestris (F, after Strasburger).

a conspicuous bud at the end of the growing season. In other cases, e.g., Araucaria and most Cupressaceae, these membranaceous bud-scales are not developed. With few exceptions, like the bald cypress (Taxodium) and the larch (Larix), whose leaves are shed annually, the conifers are evergreens, and their individual leaves persist for several years. The leaf has a single leaf trace, which may remain undivided and extend into the leaf as a single median vein or may divide at the base of the leaf, forming two veins; in some cases, e.g., Agathis, there is a repeated dichotomy resulting in numerous apparently parallel veins.

The leaf.—The pine leaf shows perhaps the most specialized structure among the Coniferales. A cross section shows the greatly thickened epidermal cells, with the stomata sunk in pits, overlying air spaces in the mesophyll, the cell walls of which show conspicuous infoldings. Below the epidermis are masses of thick-walled, hypodermal fibers. The two vascular bundles occupy the center of the section and are structurally like

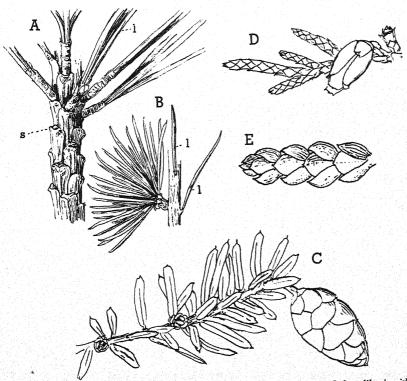


Fig. 271.—A, young shoot of Pinus Coulteri, showing leaf scars, s; B, Cedrus libani, with many-leaved fascicle; C, hemlock (Tsuga canadensis); D, Thuya occidentalis; E, Thuya plicata (E, after Pilger).

the stem bundles. Surrounding the bundles is a mass of colorless parenchyma sharply separated from the green mesophyll by the endodermis. In the mesophyll are resin ducts varying in number in different species. Sometimes, e.g., in *Pinus strobus*, there is a single vascular bundle.

In the Taxaceae, the Taxodiaceae, and the Cupressaceae the leaves are simpler in structure. There is no marked development of thickened hypodermal tissues and the mesophyll is composed of uniform parenchyma. There is a single vascular bundle.

The root.—The primary root of the seedling may persist as a taproot but is supplemented or even replaced by lateral roots, which may extend horizontally for a great distance. The primary root is usually diarch but may be at first tetrarch becoming diarch later. The secondary roots arise from the pericycle. A cambium is formed outside the ring of primary

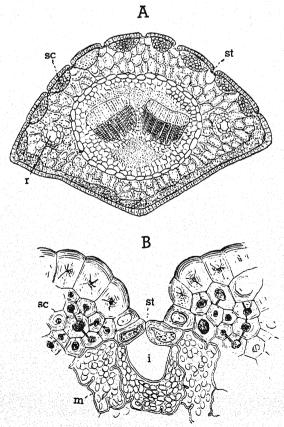


Fig. 272.—Cross section of leaf of *Pinus Coulteri*; r, resin duct; sc, sclerenchyma; st, stoma; B, stoma and surrounding tissue; sc, sclerenchyma; m, mesophyll cells.

vascular bundles and thus inaugurates a secondary growth in the thickness of the roots, much like that in the stem.

The flowers.—The flower in the conifers is in most cases a cone or strobilus recalling the sporangial cones of Lycopodium or Equisetum. Male and female inflorescences in some genera occur on the same individual, in others the plants are dioecious.

Microsporangium.—The microsporangia, or pollen sacs, are borne on special scales, recalling the sporangia of the ferns and of Equisetum. The sporophyll bearing the pollen sacs may be regarded as a stamen. The staminate strobilus may be terminal or it may be borne in the axil of a foliage leaf or a scale. The stamen usually has a narrow base of stalk and more or less expanded distal portion. The latter may be a shield-shaped

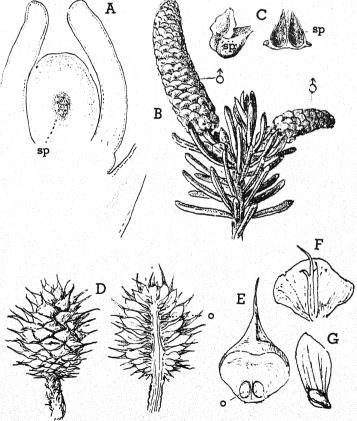


Fig. 273.—A, young ovule of Taxus baccata; sp, sporogenous cells; B, Picea orientalis, staminate cones, C; C, single stamens with pollen sacs, sp; D, young ovulate cones of Pinus virginiana; E, single scale with two ovules; F, seminal scale of Pseudotsuga taxifolia, with subtending bract; G, seed of Pseudotsuga.

body (Taxus) or it may be a flattened, leaf-like lamina. The pollen sacs are always on the lower (abaxial) surface, like the sporangia of the ferns and the cycads. In number they range from two in the Pinaceae to fifteen or more in Araucaria. In the latter they are elongated pendent bodies and the stamen recalls the sporangiophore of Equisetum. In Taxus the pollen sacs form a circle on the lower side of the peltate apex and are more or less united into a sort of synangium.

The development of the pollen sac may be compared with the sporangium of the eusporangiate fern type. In the very early stage there is a hypodermal cell layer, the archesporium, which divides into an outer layer, contributing to the anther wall, and an inner one which gives rise to the sporogenous tissue. The development of the pollen spores is like that of

the spores of the pteridophytes.

The wall of the pollen sac consists of several cell layers, the innermost contributing to the tapetum, while the outermost layer may persist as the "endothecium" and with the epidermis forms the wall of the ripe pollen sac. The other parietal cells are broken down during the later development of the sporogenous tissue. The ripe spores are in many cases provided with wings formed from the outer spore membrane.

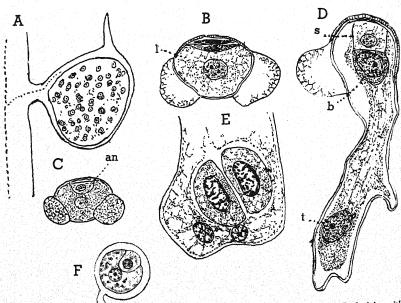


Fig. 274.—A, section of pollen sac of *Pinus excelsa*; B, pollen spore of P. laricio, with two prothallial cells; C, pollen spore of P. radiata; an, generative cell; D, germinating pollen spore of P. laricio; s, stalk cell; b, body cell of antheridium; E, pollen tube of Thuya occidentalis, with two large sperm cells; F, pollen spore of Cryptomeria japonica (A, B, D, after

Chamberlain; E, after Land).

The ripe pollen spores already show the first germination stages as they do in the cycads and in *Ginkgo*. In the Araucariaceae and in some species of *Podocarpus* there is a marked development of sterile prothallial cells; they are also found in the Pinaceae, but they are absent in the Taxaceae, the Taxodiaceae, and the Cupressaceae. In the latter forms the first division in the spore separates a small generative cell from the large tube cell. In the pines, the spore has two conspicuous wings. They are vesicles formed by a splitting of the spore membranes. The pollen sac opens either by a longitudinal fissure on the inner face or, sometimes, by an oblique transverse opening.

The ovule.—The nature of the ovulate flower has been the subject of almost endless speculation which cannot be considered here. An excellent summary of the most notable theories has been given by Coulter and Chamberlain (Gymnosperms, pp. 244 ft.).

Except in the Taxaceae and the Podocarpaceae, where they are terminal on the shoot, the ovules are borne on a definite strobilus composed of scales. The morphological character of this ovuliferous scale is the question which has aroused so much controversy. Is it the equivalent of the sporophylls of *Lycopodium* or *Selaginella*, for example, or do these ovuliferous scales represent axillary shoots (sporangiophores?) subtended by a scale-leaf?

Whatever may be the morphological nature of the ovuliferous scale, it bears upon its upper (adaxial) face, the ovules: a single one in the Araucariaceae, two in the Pinaceae, and a varying number in the Taxodiaceae and the Cupressaceae. The Pinaceae, which include the majority of the evergreens of the northern regions, have been most extensively studied. In the ripe cones of the Pinaceae the seminiferous scales are thick and woody with two seeds. The seminiferous scale is subtended by a bract, which is very conspicuous in some of the firs (Abies) and in the Douglas fir (Pseudotsuga). In the pines and spruces these scales are much less conspicuous.

In the Taxodiaceae and the Cupressaceae the subtending bract is entirely wanting and the ovules are borne directly on the scale. The advocates of the theory that the condition in the Pinaceae is primitive regard the apparently single scale of the Cupressaceae as really a fusion of the subtending bract and the ovuliferous scale of the Pinaceae.

In the Araucariaceae no trace of a subtending scale can be discovered and Seward (Fossil Botany) believes that the ovuliferous scale in Araucaria is a true sporophyll. Since the Araucariaceae are probably the oldest of the existing conifers, one might infer that the single definite sporophyll is primitive, the condition in the Pinaceae, secondary.

The theory that the ovuliferous scale represents a reduced shoot borne

in the axil of the subtending scale might be interpreted as indicating that the cone is a compound structure, or inflorescence, rather than a single flower.

As to the relation of the single terminal ovule in *Taxus* and the strobiloid conifers, there is no very satisfactory explanation. Goebel and some others consider that the *Taxus* type is a reduction from a more primitive strobiloid condition; but it seems more likely that the two types are not necessarily directly related.

The young ovule is usually a nearly hemispherical body of uniform cells and early develops a single integument. The origin of the megaspore

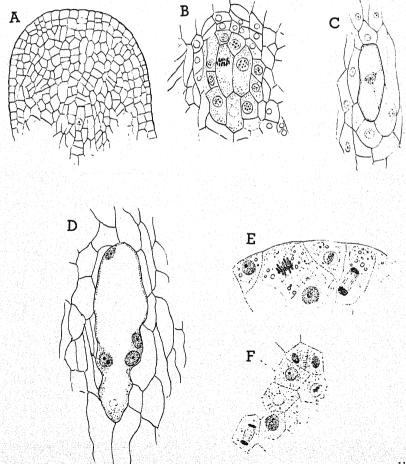


Fig. 275.—A, very young ovule of Taxus baccata; B, sporogenous tissue from an older ovule; C, young embryo sac; D, older embryo sac; E, F, cell formation in the young gameto-phyte.

(embryo sac) shows considerable variation. Strasburger found in Larix—and a similar condition has been shown in Pinus by other observers—that a single embryo sac is developed. The megaspore mother cell is formed by the division of a hypodermal cell into an outer tapetal cell and an inner megspore mother cell. The tapetal cell divides several times and the megaspore mother cell is thus pushed downward toward the center of the nucellus. It then undergoes two transverse divisions into four potential megaspores, only one of which, normally the lowest one, becomes the embryo sac. As a result of a reduction division the megaspores have the haploid

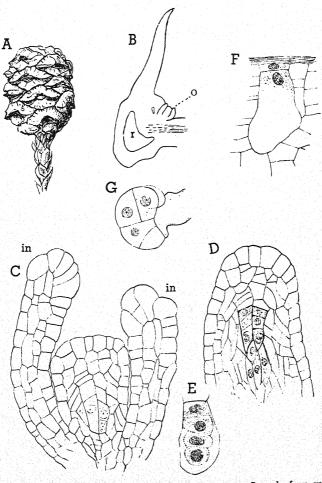


Fig. 276.—A, ripe cone of redwood (Sequoia sempervirens); B, scale from young cone, showing an ovule, o; C, section of young ovule, showing integument, in, and sporogenous cells; D, sporogenous tissue from an older ovule; E, sporogenous cell divided into four; F, young archegonium; G, young embryo (B, E, F, G, after Shaw).

chromosome number-usually 12. In Sequoia the number is 16, and in

Widdringtonia, only 6.

In the Taxaceae, the Taxodiaceae, and the Cupressaceae there are several megaspore mother cells which divide and form several spore tetrads. In *Thuja* the young spores may be arranged tetrahedrally. In the redwood (Sequoia sempervirens) Lawson states that several megaspores may begin germination but only one embryo sac reaches maturity.

With the growth of the ovule the integument extends beyond the top of the nucellus and forms an opening, the micropyle, leading to the space above the nucellus. There is no pollen chamber formed in the tissue of

the nucellus, such as is present in the cycads and in Ginkgo.

The male gametophyte.—There is a good deal of variation in the development of the male gametophyte. In the Taxodiaceae and the Cupressaceae the first division in the spore separates a generative cell from the tube cell. In the Pinaceae, the Araucariaceae, and the Podocarpaceae sterile prothallial cells are cut off before the formation of the generative cell. In Pinus there are usually two prothallial cells which are disorganized before the generative cell is formed. In Araucaria and some species of Podocarpus there is a much greater development of prothallial tissue which is persistent. There are two primary prothallial cells comparable to those in Pinus, but these undergo several divisions. Burlingame states there may be in Araucaria Braziliensis 15 to 25 prothallial cells. The walls of the prothallial cells soon disintegrate and the nuclei are discharged into the cytoplasm of the cell cavity. This marked development of the prothallial tissue in Araucaria supports the view that the Araucariaceae are the most primitive of the existing conifers.

The final development of the gametophyte takes place after the emergence of the pollen tube. The generative cell divides into the basal (stalk) cell and the body cell. The latter becomes free and migrates into the pollen tube together with the nucleus of the stalk cell. From the body cell are formed the two male gametes. These may be distinct cells or there may be no division wall between them. Unlike the male gametes of the cycads and Ginkgo these are not ciliated spermatozoids but must be carried to the archegonium by the pollen tube. Thus the last trace of the aquatic origin of the male gametes has disappeared. Burlingame, however, found that the sperms in Araucaria showed amoeboid movements. In Araucaria the free nuclei of the prothallial cells are also carried into the pollen

tube.

The development of the male gametophyte is slow and may require

more than a year before it is complete.

The female gametophyte.—While there is a good deal of variation in some details, the essential characters in the development of the female

gametophytes are the same in all the conifers that have been investigated. Like the male gametophyte the development is often very slow.

The first nuclear division occurs while the megaspore is still very small. At this time the cytoplasm fills the cell and the single nucleus is centrally placed. With the growth of the young embryo sac the cytoplasm forms a peripheral layer enclosing a large central vacuole. The nuclei at this stage are numerous and distributed through the cytoplasmic layer. The early development is thus very much like that in Selaginella, where the development of the gametophyte within the megaspore also begins before the full size of the megaspore has been reached. As in Selaginella, when the full number of free nuclei has been attained, cell walls are formed between the nuclei, resulting in a peripheral layer of cells which are open on their inner face. The further growth of the prothallial tissue is centripetal and the embryo sac is finally filled with a mass of endosperm.

Sometimes, e.g., in Sequoia sempervirens, the formation of cellular tissue is for a time restricted to the ends of the embryo sac, the median region showing only free nuclei. In Cryptomeria the primary endosperm

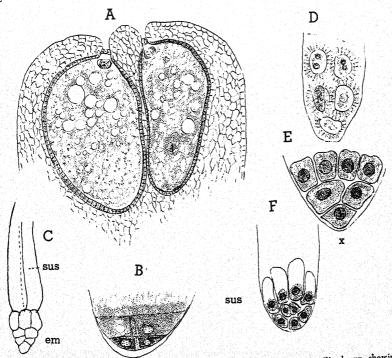


Fig. 277.—A, two archegonia of *Pinus radiata*; B, lower portion of fertilized egg, showing first divisions; C, young embryo with suspensor, sus; D-F, development of embryo in *Taxus baccata*; x, apical cell; sus, suspensor (D-F, after Jaeger).

cells may become multinucleate and may show a form of "free-cell formation," the nuclei becoming invested with individual cell membranes.

Archegonium.—The archegonium of the conifers is much like that of the cycads and Ginkgo. The first ones may appear while the gametophyte is still at a very early stage of development. The mother cell of the archegonium divides first into a superficial neck cell and an inner cell from which the egg cell is formed. The neck cell divides by a vertical wall into two cells, which may remain undivided or may form a group of several cells. In the Pinaceae there are often 8 arranged in two tiers of 4 each. Burlingame states that in Araucaria there may be 12 arranged in a single layer. Like Cycas and Ginkgo there is no neck canal cell. The central cell may have a definite ventral canal cell cut off, e.g., Pinus; but in most cases no division wall is formed between the egg and the ventral canal cell, the latter being represented only by the nucleus, which often very soon disintegrates and is difficult to demonstrate. This recalls the condition in certain eusporangiate ferns, e.g., Ophioglossum and Danaea. The bulk of the central cell remains as the egg.

The number of archegonia varies greatly. In the Pinaceae there are from one to seven, while in the Taxodiaceae there are from four to sixty and in some of the Cupressaceae there may be a hundred or more.

The central cell (egg cell) becomes very large, with a corresponding enlargement of the centrally placed nucleus. The egg cell is surrounded by a definite mantle of modified endosperm cells, which are concerned with the nutrition of the egg cell.

In the Cupressaceae the archegonia are in groups having a common endosperm mantle and they open into a common archegonial chamber. A similar condition obtains in some of the Taxodiaceae but is less constant. The redwood (Sequoia sempervirens), a member of the family, may have the archegonia either solitary or in groups.

That the embryo sac is really a spore is indicated by the very evident spore membrane which invests it. In the Pinaceae this spore membrane is double, having an outer corky layer and an inner one of cellulose. In other cases, e.g., Araucaria, there is only the cellulose layer.

In the Pinaceae the growth of the endosperm practically destroys the nucellus of the ovule, but in the Araucariaceae the outer tissue of the nucellus persists.

Fertilization.—A long period may elapse between the shedding of the pollen and fertilization. Chamberlain found in Pinus laricio that pollination occurs in June but fertilization is not effected until July of the next year. More commonly, however, fertilization takes place the same season. In the arbor vitae (Thuja) and in spruce (Picea) fertilization is effected within about a month after pollination; the hemlock (Tsuga) requires six weeks and the Douglas fir (Pseudotsuga) two months.

In *Pinus* at the time of pollination the nucellus secretes a mucilaginous substance which exudes from the micropyle and holds the pollen spores. As the moisture evaporates, the pollen is drawn into the micropyle and is finally deposited upon the summit of the nucellus, where it sends out the pollen tube which penetrates the tissue above the archegonia.

During the growth of the pollen tube the body cell of the spore divides into two, which constitute the male gametes. The pollen tube pushes through the megaspore membrane and forces its way between the neck cells of the archegonium, discharging its contents into the large egg cell.

The pollen tube does not in all cases penetrate the nucellus immediately. In Sequoia it grows for some time between the integument and the nucellus before penetrating the latter. In the Araucariaceae the pollen is deposited on the sporophyll before the ovule is formed; and for a long time grows along the surface of the sporophyll before it reaches the ovule.

Only one of the male gametes is functional; the second one, together with the tube nucleus and stalk nucleus, becomes disintegrated. The functional male nucleus comes into contact with the female nucleus, but for some time they remain distinct. Burlingame states that in *Araucaria* the cytoplasm of the male gamete is retained after the gamete is discharged into the egg and forms an envelope about the two conjugating nuclei.

The proembryo.—The two nuclei formed by the division of the fusion nucleus in nearly all forms that have been examined remain free in the cytoplasm of the fertilized egg, or zygote. Lawson found that in Sequoia the first nuclear division was followed by the formation of a transverse cell wall. In Araucaria the free nuclei continue to divide until as many as 45 may be formed before the first cell formation occurs. The proembryo is thus very much more like that of Cycas or Ginkgo than is the case in any other conifers.

In the Pinaceae and all the Taxodiaceae, except Sequoia, the first cell formation begins after four free nuclei have been formed. These four nuclei, in Pinus, pass to the base of the zygote, where they are arranged in a single plane. With the next division there is a horizontal wall formed between each pair of nuclei and thus two tiers are developed; and by further vertical walls there result two definite cell layers, the upper one open above. A second transverse wall in each cell results in a body (proembryo) composed of 16 cells arranged in four tiers. Of the three lower tiers the lowermost develops into the embryo proper; the middle tier becomes the suspensor, and the tier above it forms the "rosette." The latter is wanting in the Cupressaceae.

In Araucaria the proembryo is a nearly globular body consisting of a group of central cells, from which the embryo develops, and a layer of peripheral cells, of which the upper becomes much elongated and forms the suspensor. The lower peripheral cells form a cap covering the apex

of the young embryo. The suspensor cells grow and divide and finally fill the upper part of the zygote. The young embryo consists of a massive suspensor and a large cylindrical body without a definite apical meristem. The root apex is formed at the junction of the suspensor and the embryo; at the free end of the embryo two cotyledons develop; and between these is the stem apex. The growth of the embryo continues after the seeds are shed, even when they are not planted.

In the Pinaceae the suspensor cells become greatly elongated and twisted. In *Pinus* each of the four primary suspensor cells may form an independent suspensor bearing an embryo at its apex; or the four suspensors may become united into a single one, and only one embryo is produced. The embryo of the Pinaceae has not been followed in detail except in the very early and the latest states. There are several cotyledons each with a single vascular bundle. The primary root is diarch.

CLASSIFICATION

FAMILY 1. TAXACEAE

In Pilger's classification of the Coniferales (Engler and Prantl, second edition), the yew family, Taxaceae, includes only three genera, *Taxus, Torreya*, and *Arthrotaxis*. Except for the latter, a monotypic genus from New Caledonia, the Taxaceae are confined to the Northern Hemisphere.

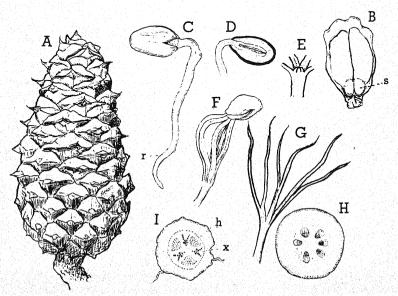


Fig. 278.—A, ripe cone of *Pinus virginiana*; B, seed scale; C-C, germination stages; D, section of seed, showing cotyledons surrounded by endosperm; E, median section of seedling; H, section of stem of seedling; I, section of root; x, xylem; h, phloem.

The common yew, Taxus baccata, is found in many parts of Europe. It grows very slowly, and many very old specimens occur in the British Islands. The wood is very hard and tough. Two similar species are found in the United States: T. canadensis in the East, and T. brevifolia in the Pacific region. These are sometimes considered to be merely subspecies of T. baccata. They are usually hardly more than shrubs. The second genus, Torreya, includes five species of very limited distribution. Of these, T. californica is confined to the Pacific Coast and T. taxifolia to Florida. The other species are found in Japan and China.

The foliage of Taxus is much like that of the firs and spruces—flattened needles arranged spirally on the shoot. The leaf structure corresponds in the main with that of the Pinaceae; but the leaf is softer in texture, owing to an almost complete absence of schlerenchyma. Torreya californica, not uncommon in the coastal forests of California, is sometimes a very large tree. The leaves are much longer and stiffer than those of Taxus. The anatomy of the stem in Taxus is much like that of the Pinaceae, though there are no resin ducts but only scattered isolated cells with resinous contents. The secondary tracheids in addition to the bordered pits may have also spiral thickenings.

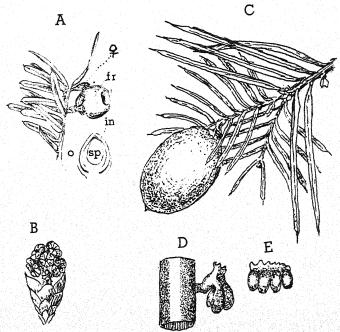


Fig. 279.—A, Taxus baccata; fr, fruit; o, section of ovule; in, integument; B, staminate cone of Taxus; C, Torreya californica; D, E, stamens of Torreya nucifera (D, E, after Pilger).

Flowers.—The Taxaceae are dioecious. The small staminate cone is in the axil of a leaf and at the base has several sterile scales. The stamen in Taxus has a short stalk and a peltate disc, with the coherent pollen sacs surrounding the margin. In Torreya the male cone is larger than in Taxus and the four pollen sacs are pendent from the somewhat irregular terminal disc. The pollen spores have no prothallial cells, the first division separating the generative cell from the tube cell.

The solitary ovule of *Taxus* is terminal on a shoot, and no strobilus is developed. According to Pilger, the ovular shoot is formed as a lateral branch from the main shoot. In *Torreya* the ovules are in pairs situated in the axils of small leaves at the base of a shoot which later continues its growth.

The archesporial tissue in *Taxus* occupies the central region of the young ovule. Apparently there are several potential embryo sacs, but usually only one of these reaches maturity. The embryo sac in the Taxaceae does not show a definite megaspore membrane such as occurs in the Pinaceae, but the development of the female gametophyte is much the same.

The basal part of the integument in *Taxus* is adherent to the nucellus, but the upper free portion forms the micropyle. About the time of pollination a second envelope forms at the base of the ovule and develops into a bright red fleshy cup, the "aril," surrounding the seed. Whether or not the aril represents a second integument is a question. In *Torreya* there are two integuments, of which the outer one becomes fleshy and forms the outer tissue of the large plum-like seed. This recalls the seeds of the cycads or *Ginkgo*.

The embryo.—In Taxus the nucleus of the zygote divides until there are 16 free nuclei, after which cell walls are formed and the zygote forms a solid cellular body, the proembryo. The embryo in the ripe seed is relatively smaller than in the Pinaceae and is surrounded by a mass of endosperm.

FAMILY 2. PODOCARPACEAE

The Podocarpaceae, unlike the Taxaceae, are predominantly austral, only a few species, relatively, occurring north of the Equator. Species of *Podocarpus* reach the West Indies and Central America, and in Asia they extend to southern Japan and the Philippines. The family includes about a hundred species, the majority belonging to *Podocarpus*. Of the other six genera, three are monotypic and one, *Phyllocladus*, is sometimes made the type of a separate family, Phyllocladaceae. Some of the species are only shrubs but others are trees of large size.

Anatomy.—The stem structure of Podocarpus is much like that of the

Taxaceae, the resin ducts being replaced by isolated resin cells. The leaves, in most cases, are rigid, like those of the Pinaceae, and there are several layers of thick-walled hypodermal cells. Except for the broad-leaved species of *Podocarpus* (Sec. *Nageia*) there is a single median vascular bundle beneath which is a resin duct.

The leaf.—The leaves vary in size and form. They may be flattened needles like those of the firs, or lanceolate with a conspicuous midrib. In a few species of Podocarpus the large broad leaves with parallel veins recall the leaflets of certain cycads, or Agathis. In other forms, e.g., Dacrydium, the short thick scale-like leaves are somewhat like those of Sequoia or some of the Cupressaceae. Sometimes both linear and scale leaves occur—e.g., Dacrydium—the linear leaves near the base of the shoot and the imbricated scale leaves in the apical region.

Flowers.—As a rule the Podocarpaceae are dioecious. The stamens usually form a definite strobilus, with several sterile leaves or bracts which may protect the young stamens. Each stamen has two pollen sacs and

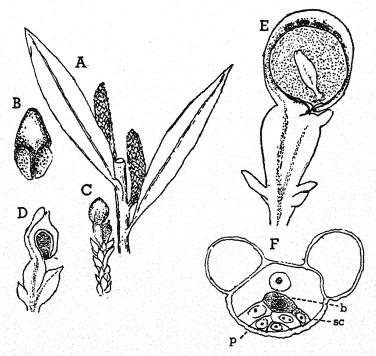


Fig. 280.—A, Podocarpus macrostachyus, with male inflorescence; B, a single stamen; C, ovulate flower of P. dacrydioides; D, section of the ovule of P. Veillardii; E, section of ripe seed of P. dacrydioides; F, pollen spore of P. Totara, showing several prothallial cells, p; b, body cell; sc, stalk cell ((A-E, after Pilger; F, after Burlingame).

somewhat resembles the stamens of the Pinaceae. The pollen sacs open by an oblique or transverse cleft. The male flowers may be terminal on an ordinary shoot, but more commonly they are borne on special dwarf branches which arise singly in the axils of foliage leaves; or they may be in clusters on special branches. In the latter case there is a certain resemblance to the male inflorescence of *Cordaites*. The pollen spore of *Podocarpus* has two wings like those in *Pinus*, and all of the other genera, except *Saxegothaea*, also have winged spores, but there may be three or more wings.

The ovule.—The ovule in the Podocarpaceae is solitary. In the simplest cases, e.g., Podocarpus spicatus, the ovules are borne at the base of small scales, or carpels, which are attached at intervals to a slender shoot,

thus forming a spike.

More often, in *Podocarpus*, the axis bearing the carpels is short and has only one or two carpels, and the ovule appears to be terminal. In *Saxegothaea* the carpels form a definite strobilus at the apex of a leafy shoot. In *Dacrydium* there may be only a solitary carpel.

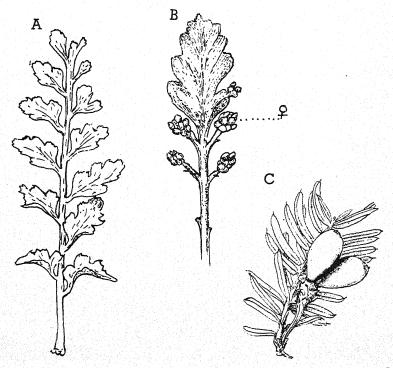


Fig. 281.—A, Phyllocladus trichomanioides, with leaf-like branches (phylloclades); B, P. glaucus, with ovulate strobili, \mathfrak{P} ; C, Cephalotaxus Fortunii.

The ovule may be either erect or bent over toward the base of the carpel. There is a single integument, which is free from the nucellus; and there is also a second envelope, the "epimatium," which may completely enclose the ovule or may be reduced to a small basal sheath. The epimatium has been compared to the aril of Taxus. In Podocarpus the epimatium becomes thick and fleshy, recalling the outer integument of Torreya. The integument develops a hard stony layer, much as in Torreya. So far as is known, the development of the female gametophyte is much like that of Pinus.

Embryo.—The embryology of the Podocarpaceae is still very incompletely known. Coker, who investigated the development in *Podocarpus coriaceus*, states that it is intermediate in character between the Araucariaceae and the Pinaceae.

The division of the fusion nucleus results in 16 free nuclei as in Taxus. The proembryo when it begins to penetrate the endosperm is composed of three tiers of cells like the Pinaceae, but the number of cells is much greater. At the tip of the proembryo is a single cell, as in Taxus, and from this the embryo proper arises. The primary embryo cell divides into two and probably into four similar cells. The frequent occurrence of more than one embryo indicates that each of the secondary embryo cells is capable of developing into an embryo, although as a rule only one reaches maturity.

The genus *Phyllocladus* differs so much in appearance from the other Podocarpaceae that it is sometimes placed in a special family, Phyllocladaceae. The remarkably leaf-like phylloclades recall the fronds of some ferns.

There are seven species, of which three are peculiar to New Zealand and the others are found in New Guinea, Borneo, the Moluccas, and the Philippines. They are shrubs or small trees. The leaves of the seedling are flattened green needles, which are gradually replaced by the rudimentary scale leaves of the older plant, and the development of phylloclades.

FAMILY 3. ARAUCARIACEAE

There has been much controversy as to the relative antiquity of the families of the Coniferales; but on the whole the Araucariaceae seem to be the most primitive of the existing conifers. Like the Ginkgoales they were once practically cosmopolitan; but now they are few in number, with only two genera, Araucaria and Agathis, and are restricted to the Southern Hemisphere and the adjacent Malayan regions. Agathis, with about twenty species, includes the Kauri pine (A. australis) of New Zealand and other species in northern Australia, New Guinea, and Melanesia (Fiji, New Caledonia) and extending to the Philippines. The species of Araucaria are mainly restricted to Australia and the adjacent islands; but two species

occur also in South America—A. Araucaria (= A. imbricata) in Chile and A. braziliensis. The Norfolk Island pine, A. excelsa, is a common greenhouse plant often grown in California, as are A. araucana, the "monkey puzzle" and the Australian A. Bidwillii.

The growth of these trees is very symmetrical, the branches of each season forming a regular whorl at each node. As the trees grow older in some species, e.g., A. Bidwillii and A. braziliensis, the early branches are shed and the closely set apical circles form an umbrella-like crown topping the tall bare trunk.

In Agathis the young tree is also very symmetrical in its growth; but later the early branches fall off, leaving smooth scars, and the mature tree

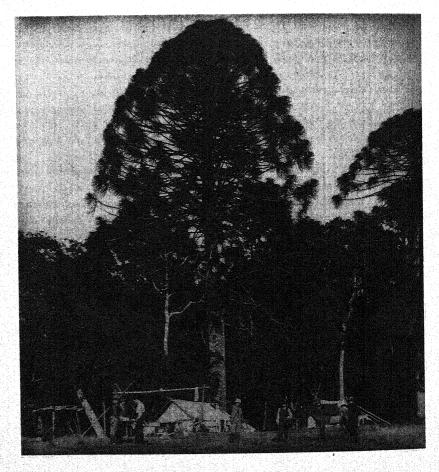


Fig. 282.—Araucaria Bidwillii, Queensland, Australia

has a massive, smooth, cylindrical bole—sometimes 20 to 30 meters high and dividing at the summit into several large branches which form an immense spreading crown.

The leaves of Araucaria are sessile and completely cover the shoot. They may be lanceolate with several parallel veins, e.g., A. Bidwillii; or smaller with a single vein, e.g., A. excelsa.

The broad leaves of Agathis, which recall those of some species of Podocarpus, are much less crowded than the leaves of Araucaria and are sometimes opposite. The leaves taper at the base, sometimes having a short petiole. Alternating with the veins are secretory ducts (resin ducts?). There is a definite palisade tissue.

The stem.—The wood of the Araucariaceae is very characteristic. The tracheids have several rows of bordered pits which are much crowded instead of the one or two single rows found in most coniferous wood. Fossil wood of the Araucarian type is abundant from the Late Palaeozoic and Mesozoic. This fossil wood has been called Araucarioxylon; but as Cordaites shows a similar wood structure and probably other Palaeozoic types, this does not prove that Araucariaceae existed prior to the Mesozoic. It may be noted that Botrychium, a fern, has tracheids resembling those of Araucaria.

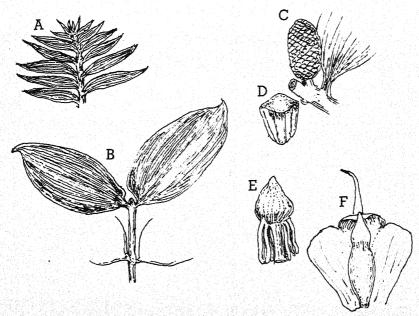


Fig. 283.—A, Araucaria Bidwillii; B, Agathis robusta; C, staminate strobilus of Agathis alba; D, single stamen; E, stamen of Araucaria araucana; F, ripe seed of A. Cunninghamii (all figures after Pilger).

Among the most remarkable fossils of the Araucarioxylon type are the giant trunks of the Petrified Forest in Arizona. These are Triassic in age and the perfectly preserved wood is practically identical in structure with that of the living Araucariaceae. Unfortunately nothing is known of their foliage or reproduction.

The flower.—The Araucariaceae are usually dioecious, but sometimes in Agathis male and female flowers occur in the same individual. The staminate cone is much larger than in most conifers. According to Burlingame it may reach a length of 15 centimeters, recalling the smaller cycads rather than the typical conifers. Burlingame estimated that in A. braziliensis there might be over one thousand stamens, each bearing ten to fifteen pollen sacs. The male cone in Agathis is smaller, and the number of pollen sacs in each stamen is less.

The early stages of the female cone are imperfectly known. It consists of a large number of ovulate scales, each with a single ovule which at maturity develops into a very large seed, which is embedded in the scale. Above the cavity containing the seed is a ligule recalling that of *Isoetes*. The tip of the scale may form a conspicuous spine like that in many pine cones. The ripe cone may be very large. In A. bidwillii it is sometimes 28 centimeters in length. The large embryo, which is surrounded by abundant endosperm, has two elongated cotyledons.

Relationships.—There has been some controversy as to the relationships of the Araucariaceae and the Pinaceae and their relative antiquity. Some students of the conifers, especially Jeffrey, believe that the Pinaceae are the older and that the Araucariaceae are derived from them. With fuller knowledge of the reproduction of the Araucariaceae and their geological history, it now seems pretty certain they are the more primitive forms from which the Pinaceae have, perhaps, been derived. If the two families are really related it is probable that the divergence of the two families was a very ancient one.

The derivation of the Araucariaceae (and perhaps of all the Coniferales) from the Lycopodineae has been suggested, the latest advocate of this theory being Hagerup. This theory, however, offers very serious difficulties and is not generally accepted. It has also been thought that their nearest fossil relatives are the Cordaitales, whose stem anatomy and leaves have much in common with the Araucariaceae. The flowers of the two, however, are radically different, and if any relationship does exist it must be extremely remote.

Geological history.—There is good evidence that the Araucariaceae, or at least forms related to them, already existed in the Permian and possibly even earlier. During the Mesozoic, like the cycads and the Ginkgoales, they were widespread in both the Northern and the Southern hemispheres. Even in the early Tertiary evidence of their existence in the Northern Hemisphere has been found.

FAMILY 4. CEPHALOTAXACEAE

This small family has only about half a dozen species, found in south-eastern Asia, including southern China and Japan. Except for the monotypic Amentotaxus argotaenia from western China, they all are species of Cephalotaxus. The best-known species, C. drupacea, is sometimes planted in the warmer parts of the United States. It is a large shrub or small tree, in general appearance resembling Taxus or Torreya. The flowers, however, are very different. Cephalotaxus is dioecious.

The stamens are borne in clusters in the axils of the leaves, the group of stamens being surrounded by several broad bracts. Each stamen has three pendent pollen sacs. The female flower is a short strobilus borne at the end of a short branch. The ovules are in pairs at the base of the thickened carpellary scales, which are more or less coherent with each other and with the axis of the strobilus.

The ripe seed is in some respects like that of *Podocarpus*. It is a pear-shaped body with a fleshy outer coat derived from the outer part of the integument. The embryo has two large cotyledons, which usually remain within the seed coat after germination.

FAMILY 5. PINACEAE

At least fifty per cent of the living conifers belong to the Pinaceae. They are practically confined to the Northern Hemisphere and for the most part to the Temperate Zone. Some of the pines and spruces reach beyond the Arctic Circle and to the timber line of the higher mountains. Only one species, *Pinus Mercusii*, which grows in Sumatra, crosses the Equator.

The great majority of the evergreens of the North Temperate Zone—the pines, firs, spruces, etc.—are Pinaceae. These are often gregarious, covering large areas, sometimes with a single species. They are the most important timber trees, as their easily worked soft wood and large unbranched trunks afford unexcelled timber for building purposes.

They reach their maximum development in the mountain forests of Pacific North America. In these mixed coniferous forests the trees may reach gigantic size. Douglas firs, sugar and yellow pines, Sitka spruces, and several species of fir sometimes are 200 to 300 feet high, almost rivaling the giant redwoods. These trees normally retain an unbranched trunk and the lateral branches are often in regular circles or tiers, so that their growth is very symmetrical, like that of Araucaria. As the trees grow old, or conditions for growth are unfavorable, there may be irregular branching; and in some species, e.g., the Italian stone pine, the leading shoot is lost and the broad crown is composed of numerous branches.

The leaf.—The leaves of the Pinaceae are slender needles, either solitary and arranged spirally on the shoot or borne in fascicles upon special dwarf shoots—e.g., Pinus, Cedrus, and Larix. In the firs and spruces the needles are usually more or less flattened and may be arranged in two rows. In the pines the leaves on the main shoot are reduced to thin scales in the axils of which are borne the special shoots bearing the fascicle of leaves, which may be two to five in number or exceptionally single. In the true cedars (Cedrus) and the larch (Larix) the number of leaves in a fascicle is much larger (30 to 40 in Cedrus). In Larix the leaves are shed annually, but in all the other genera they are evergreen and may be retained for many years.

The flowers.—The Pinaceae are typically monoecious. The two sorts of flowers may be on separate shoots or they may be borne close together. The staminate strobilus is composed of closely imbricated scales (stamens), which are sometimes colored red or yellow. The tip of the stamen is bent upward, and there are two pollen sacs lying close together on the abaxial surface of the stamen.

The ovulate strobilus consists of thick scales with two ovules on the adaxial surface near the base. The ovuliferous scale is subtended by a scale, which is inconspicuous in *Pinus* but in some species of fir (*Abies*) and the Douglas fir (*Pseudotsuga*) may extend beyond the seed scale. The seed scales become hard and woody in the ripe cone, which attains a large size in some of the firs and pines. The sugar pine (*P. Lambertiana*) has pendent cones, sometimes 50 centimeters in length. The ripe seeds are provided with a membranous wing formed from the superficial tissue of the scale.

Classification.—Pilger includes in the Pinaceae nine genera, viz., Abies, Keteleeria, Pseudotsuga, Tsuga, Picea, Larix, Cedrus, and Pinus.

The firs (Abies), with about forty recognized species, are predominantly mountain forms but also grow at lower elevations in their northern range. The species are distributed throughout the North Temperate and sub-Arctic regions. In North America the majority of the species belong to the Pacific area. In the Eastern states only two species occur, of which the balsam fir, A. balsamea, is widely distributed through the Northern states and Canada from Labrador to the Northwest Territory. In the Pacific coastal and mountain forests the giants of the genus occur, e.g., A. concolor, A. magnifica, and A. grandis.

The second genus, *Keteleeria*, is much like *Abies*, but its seed scales remain attached to the axis of the cone. There are three or four species found in China.

Pseudotsuga taxifolia, the Douglas fir, the most important timber tree of the Pacific Coast, is also one of the largest of the conifers. It reaches its

maximum development in Oregon and Washington and is abundant also in British Columbia.

In habit the Douglas fir is much like the true firs (Abies), but the pendent cones recall the spruces (Picea). The cones may be immediately recognized by the very conspicuous three-pronged bracts between the seed scales.

Among the most characteristic of the American conifers are the hemlocks (Tsuga), with two Eastern and two Western species. The common Eastern hemlock, T. canadensis, is abundant in the Northern states and Canada from the coast to the Great Lakes. Along the mountains southward it reaches to Alabama. Of the Pacific Coast species, T. heterophylla is abundant from southern Alaska along the coast to northern California. In the high mountains the second species, T. Mertensiana, extends to the timber line. About ten other species are Asiatic, from the eastern Himalayas to China and Japan.

The leaves are attached to a small cushion and leave a scar when they fall. The cones are small and pendent at the end of slender twigs.

The spruces (*Picea*) resemble in habit the firs, differing from them in the cones, which are pendent, with the seed scales remaining attached to the axis of the cone. The familiar Norway spruce, *P. excelsa*, often planted for ornament, is native in many parts of Europe and extends to Russia and Siberia, reaching beyond the Arctic Circle in some localities. In America the spruces are especially trees of the northern areas or high mountains. *P. canadensis*, the white spruce, reaches to latitude 68° in Alaska, and in the boggy areas of northern Canada and Alaska the spruces form extensive forests. In the Rocky Mountains, *P. Engelmannii* reaches to timber line—3,300 meters.

Of the Pacific Coast species the most important is the Sitka spruce, *P. sitchensis*, which is one of the largest trees in the coastal region from Alaska to northern California.

The larches (*Larix*), like the spruces, are mostly inhabitants of the colder parts of the Northern Hemisphere. Mostly trees of moderate size, they are less symmetrical in growth than most of the Pinaceae, from which they differ also in having deciduous foliage.

Of the ten known species four are American. The tamarack of the Eastern states, *L. laricina*, grows in cold swamps in the Northern states and Canada. *L. occidentale* of the northern Rocky Mountains of Montana and Idaho is a large tree yielding valuable timber.

The name cedar is often applied to a number of Cupressaceae, e.g., *Juniperus* and *Thuja*; but the true cedars, *Cedrus*, are only four in number. The best-known are the cedar of Lebanon from Asia Minor, *C. Atlantica* from the Atlas Mountains, and *C. Deodara* from the Himalayas. These

are often grown in California. The species are closely related and sometimes are regarded as varieties of a single species.

Pinus, the largest genus of the Coniferales, has about one hundred species, distributed over the whole North Temperate Zone and in a few cases penetrating the tropics. P. insularis, a Philippine species, is abundant in the mountains of Luzon, and other species occur in the mountains of Mexico and Central America and some of the West Indies.

In the United States the genus is well represented. The white pine, *P. strobus*, once the most important timber tree of America, has been nearly exterminated through the ravages of the lumberman in most of its former range.

In the forests of the Sierra Nevada and the Cascades there is found the largest of all the pines, the sugar pine, *P. Lambertiana*, sometimes 250 feet high, with a trunk diameter of ten feet. The cones are the largest of any of the conifers. Another giant pine of the Pacific region is the Western yellow pine, *P. ponderosa*, almost rivaling the sugar pine in size. The yellow pine has a wide range, reaching to the Rocky Mountains and southward into Lower California. Even more widely distributed is the lodge-pole pine, *P. contorta*, which extends along the Pacific Coast from Alaska to California, and in its mountain form, var. *Murryana*, one of the commonest trees of the whole Rocky Mountain area.

The commonest European species is the Scotch pine, *P. sylvestris*, found in most parts of Europe and much of northern Asia. A number of other species are found in central and southern Europe, e.g., *P. laricio*, *P. cembra*, and *C. pinea*, the Italian stone pine.

Flowers.—The staminate flowers are small oblong strobili replacing branches at the base of the terminal shoot. Each stamen has two pollen sacs, and the pollen spores have the characteristic inflated wings. The ovulate scales are thick, and the subtending scales are inconspicuous, finally disappearing completely. In the ripe cone the seed scales are thick and woody. In the white pine and the sugar pine the cone is elongated and the scales are loosely imbricated, the rounded scales being relatively thin. In most species they are much thickened at the margin and are tightly packed together, sometimes remaining closed for years. Seen from the surface, the scales are rhomboidal in outline with a central prominence, the "umbo," which may develop into a thick hooked spine (P. Coulteri).

The genus has been divided into two subgenera: (1) Haploxylon, in which there is a single vascular bundle in the leaf; and (2) Diploxylon, where there are two bundles. Haploxylon includes the white pine, the sugar pine, and several others which with few exceptions have the leaves in fives. Diploxylon includes a large majority of the species; in these the leaves are more rigid than in the white pines and the leaves are mostly in clusters of 2-3, although there are some exceptions.

FAMILY 6. TAXODIACEAE

The Taxodiaceae, with about a dozen species belonging to eight genera, include the largest and oldest of living trees. The giant sequoias of California and the Mexican Taxodium mucronatum have no rivals, some individuals being possibly 4,000 years old. They are greatly restricted in their distribution at present, but the fossil record shows that they are relicts of once much more widely distributed genera. Sequoia, the two living species of which are practically confined to California, was once abundant over much of the Northern Hemisphere. The bald cypress (Taxodium distichum) of the Gulf states was in Tertiary times common in many localities both in North America and Europe, represented apparently by an identical species.

Like the Pinaceae, the Taxodiaceae are mainly inhabitants of the North Temperate Zone. One genus, *Arthrotaxus*, occurs in Tasmania; but it is possibly related more nearly to the Cupressaceae than to the other Taxodiaceae.

Sequoia sempervirens, the redwood, is found near the coast of California from about a hundred miles south of San Francisco to the Oregon line. In northwestern California it sometimes forms pure stands of considerable extent and reaches its maximum size. Trees exceeding 350 feet have been measured, the tallest trees of which authentic records have been made. The big tree of the Sierra Nevada, S. gigantea, occurs in scattered groves mixed

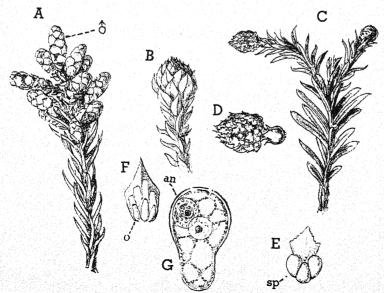


Fig. 284.—A, Cryptomeria japonica; &, staminate cones; B, ovulate cone of Cryptomeria; C, D, Sequoia sempervirens, with staminate strobili; E, stamen of Sequoia; F, ovulate scale of Cryptomeria; G, germinating pollen spore of Cryptomeria.

with other conifers at elevations of 5,000-7,500 feet. None of the trees are quite as tall as the coast redwood but they have larger trunks.

The leaves of the redwood are of two kinds. On the terminal shoots they are short pointed scales; but on the lateral shoots they are flattened needles arranged mostly in two rows along the flanks of the small twigs, which finally are shed, with the attached leaves. In S. gigantea the leaves are all closely set, pointed scales.

The small staminate strobilus of *Sequoia* may be terminal on a short branch or may be in the axil of the upper leaves. The stamen is a broad scale, with usually three pollen sacs at the base. The pollen spore has no prothallial cells.

The ovulate strobilus is at the apex of a short branch. At a very early stage there is a small subtending scale which soon fuses with the ovulate scale, which has at its base several erect ovules which later bend toward the base of the scale. The free end of the scale is thickened very much like that of many pines.

Several megaspores are formed in Sequoia, but usually only one reaches maturity. The membrane of the embryo sac is less developed than in the Pinaceae, but the development of the gametophyte is much the same except that the first division of the fusion nucleus in the zygote is followed by a division wall. The archegonia are numerous, sometimes as many as 60. They may be in groups or sometimes solitary. The number of neck cells in Sequoia is 2-4. The development of the embryo is much like that of the Pinaceae, and there are several (4-6) cotyledons.

The second American genus, *Taxodium*, the "bald cypress" of south-eastern United States, is the type of the genus, which includes a second species of the same region; and the Mexican *T. mucronatum*, while never equaling the *Sequoias* in height, may surpass them in the size of the trunk. The famous big tree of Tule near Oaxaca in Mexico is estimated to be of equal age with the oldest of the California big trees.

Taxodium distichum grows in swamps, often with the base of the trunk completely submerged. It is a very characteristic feature of the swamps of the lower Mississippi, overtopping the other trees. The base of the trunk is greatly enlarged, and from the roots peculiar conical structures ("knees") extending above the water level are supposed to be aerating organs for the submersed roots. The old trees have very irregular branching crowns.

The terminal shoots have slender scattered leaves, but for the most part the leaves are borne on slender lateral twigs, like those of the redwood, which was first described as a species of *Taxodium*. The leafy twigs of *Taxodium distichum* are shed each season and the tree is bare in winter. The Mexican species is evergreen.

The numerous staminate flowers are borne on special elongated slender shoots, forming a sort of inflorescence. Each stamen bears 5–9, nearly globular, pollen sacs. The ovulate strobilus resembles that of Sequoia, but there are only two ovules. As the scale develops it becomes much thicker and the seeds become enclosed in a cavity at the base of the scale and are fused with its surface.

Classification.—Besides Sequoia and Taxodium there are six genera, five of which are confined to eastern Asia; the other, Arthrotaxus, from

Tasmania, is doubtfully associated with the other Taxodiaceae.

Of the eight genera recognized by Pilger, the first, Sciadopitys, differs so much from the others that it is sometimes made the type of a separate family. The only species, Sciadopitys verticellata, a native of Japan, is sometimes seen in cultivation.

The shoot shows a regular succession of nodes and internodes. The leaves are reduced to small scales, which at the nodes develop from their axils flattened, leaf-like shoots or "cladodes," which function as leaves. The cladodes resemble true leaves in their anatomy and it has even been suggested (Strasburger) that the cladode represents a shoot bearing two united leaves, comparable to a two-leaved pine fascicle with the leaves coalescent.

Cryptomeria Japonica is indigenous in Japan, where it is also planted extensively. It is a tree of great size, in appearance much resembling Sequoia, from which it differs in several respects. The embryo has only two cotyledons. The avenue of Cryptomerias leading to Nikko and the groves of ancient trees about the temples and shrines form one of the famous sights of Japan. A second species has been found in South China.

Taiwania cryptomerioides is a large tree from the mountains of Formosa and southern China. It is said to resemble closely Sequoia and Cryptomeria; but its cones are quite different, the scales having only two

seeds, or even a single one. The embryo has two cotyledons.

Cunninghamia has two species: C. sinensis, a small tree from southern China; and C. Konishii, a large tree from Formosa, which grows with Taiwania. The leaves are larger than in any other of the Taxodiaceae.

Fossils.—Fossils very similar to the living species of Sequoia are abundant in Cretaceous and Tertiary formations throughout the North Temperate Zone. In Cretaceous rocks of Spitzbergen and Greenland remains of Sequoia have been found, and recently Chaney has reported discovery of abundant remains of redwoods in some of the western Aleutian Islands. The oldest fossils referred to Sequoia are Jurassic.

Like Sequoia, Taxodium was once common throughout the North Temperate Zone in both America and Eurasia. Throughout the Tertiary, species

hardly distinguishable from the living T. distichum were found.

Sciadopitys is evidently a very old type. S. tertiaria, according to Kräusel, from Miocene formations in the Rhine district, is very close to the living species; but much more ancient forms have been described from the Cretaceous and Upper Jurassic of Greenland, the Middle Jurassic of Norway, and the Rhaetic of Sweden.

FAMILY 7. CUPRESSACEAE

The Cupressaceae form the second largest family of the Coniferales. The family is practically cosmopolitan, having many representatives in both the Northern and Southern hemispheres. Of the 15 genera, 6 are restricted to the Southern Hemisphere and 8 to the Northern, and one genus, Libocedrus, has species both north and south of the Equator.

The largest genus, Juniperus, is the most widespread, occurring in almost every part of the North Temperate and sub-Arctic zones. Thuja and Chamaecyparis have species in both Atlantic and Pacific North America and in eastern Asia, but do not occur in Europe. The true cypresses (Cupressus) are found in Pacific North America and in Asia from China to the Mediterranean.

The austral genera are much more restricted in their range. The largest genus, *Callitris*, is confined to Australia and the neighboring islands. *Widdringtonia* is found only in South Africa. Several genera are monotypic, viz.: *Fitzroya*, peculiar to Chile; *Actinostrobus*, of West Australia; and *Diselma*, from Tasmania.

The Cupressaceae, for the most part, are shrubs or trees of moderate

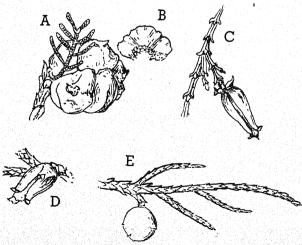


Fig. 285.—A, ripe cone of Cupressus macrocarpa; B, scale from young cone, with numerous ovules; C, Libocedrus decurrens; D, Thuya occidentalis; E, Juniperus virginiana.

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size. There are, however, some large trees. In the Pacific area of the United States and Canada the incense cedar, Libocedrus decurrens, and the giant Arbor vitae, Thuja plicata, locally called cedar, are among the largest trees. The Chilean Fitzroya cupressoides also reaches a great size.

Anatomy.—The general structure of the stem in the Cupressaceae resembles that of the Taxodiaceae. There are no resin ducts in the wood, but there are numerous individual resin cells. Resin ducts may be formed in the primary phloem.

The leaves in the seedling are slender needles, and this condition may be permanent, e.g., as in *Juniperus communis*. In the greater number of species the leaves are closely set, small, thick scales, which are either opposite or in whorls of three. These leaves are decurrent, so that the surface of the shoot is completely hidden. The mesophyll is composed of uniform cells and there is a single vascular bundle between which and the lower epidermis there is usually a resin duct.

Flowers.—The Cupressaceae are mostly monoecious, with the staminate and ovulate flowers close together. The stamens form small cones at the tips of short branches or sometimes are borne in the axils of leaves. The stamens, like the foliage leaves, are in pairs or in whorls of three. No prothallial cells are developed, and the ripe spore has only the generative and tube cells.

The ovulate scales also form a strobilus, which is much simpler than that of the Pinaceae. In the greatly reduced strobilus of *Juniperus* the fertile scales may sometimes be reduced to a single one, so that the ovule appears to be a terminal structure. There is no trace of the subtending scale of the Pinaceae. The ovulate scales may be more or less completely fused, and in *Juniperus* the ripe cone forms a solid, berry-like "fruit."

In general, the development of the male gametophyte is like that in the Taxodiaceae and two male gametes are formed. It has been found, however, that in some species of *Cupressus* the body cells may give rise to a larger number of gametes. Juel found in *C. Goviniana*, a California species, 4–20 gametes, and in *J. communis* sometimes 4. Doak reports 12 gametes in *C. arizonica*. Except for *Microcycas* these are the only known exceptions to the two male gametes found in all other gymnosperms.

The development of the female gametophyte is much like that of the Pinaceae and the Taxodiaceae. Like the latter, the archegonia are in groups, the whole complex being surrounded by a common mantle of endosperm cells. The number of archegonia in *Juniperus communis* is 4–10. In another genus, *Widdringtonia*, there may be over a hundred. The neck cells are 2–8 in number and sometimes are disorganized before fertilization occurs. As in the Taxodiaceae, no division wall separates the egg nucleus and the ventral canal cell nucleus.

Embryo.—The proembryo in Thuja, Juniperus, and Cupressus has 8 free nuclei before the first cell walls are formed. In Juniperus several embryos may begin to develop, but in Thuja only a single embryo is formed.

Classification.—The fifteen genera recognized by Pilger are grouped in three subfamilies, viz., Thujoideae, Cupressoideae, and Juniperoideae.

SECTION I. THUJOIDEAE

Of the eleven genera included in the Thujoideae, only two, Thuja and Libocedrus, are found in North America. The former is represented in eastern United States by the "white cedar," T. occidentalis; in the Pacific region is the giant T. plicata, one of the largest trees of the Pacific forest, extending from southern Alaska to northern California.

The staminate flowers are terminal and composed of 4-6 stamens. There are 3-4 pollen sacs. The ovulate cone is composed of several decussate pairs of scales, of which 2-3 pairs are fertile, each scale having two erect ovules. The embryo has two cotyledons.

The incense cedar, Libocedrus decurrens, is the only North American species. The other eight species are found in Chile, New Zealand, New Guinea, and China.

The most important genus of the Thujoideae in the Southern Hemisphere is *Callitris*, with about twenty species in the Australian region. They are mostly shrubs or small trees. They are densely branched, the slender branchlets recalling the sterile shoots of *Equisetum*. The leaves are usually in whorls of three and are grown together, much like the sheaths of *Equisetum*.

Among the other genera of the Thujoideae are Actinostrobus, with two species restricted to West Australia, and Widdringtonia, with five species in South Africa. Fitzroya cupressoides, the only species, is a large tree from southern Chile, greatly prized for its timber.

SECTION II. CUPRESSOIDEAE

The two genera of the Cupressoideae, Cupressus and Chamaecyparis, belong exclusively to the North Temperate Zone. Cupressus has about a dozen species, of which the majority are found in Pacific North America, in very restricted areas from Mexico and Central America to northern California. The so-called "Italian" cypress, C. sempervirens, is a characteristic feature of the Mediterranean landscape, where it was introduced in very early times from Asia Minor or Persia. It is often planted also in California. Other species are found in eastern Asia, from China to the Himalayas.

The best known of the California species is C. macrocarpa, the Monterey cypress. This is restricted to two headlands on the California coast south of Monterey. It is very commonly cultivated in various warm temperate climates like New Zealand, South Africa, and Chile, and in southern Europe. The cypresses are mostly trees of moderate size, densely branched, the slender twigs with closely imbricated small scale-leaves. The ripe cones are globular and the thick scales are closely fitted together. There is a conspicuous "umbo" in the center of the polygonal face of the scale.

Chamaecyparis resembles Cupressus in its essential characters; but the habit of the tree is more like that of Thuja, the twigs being similarly flattened and the branches having a similar frond-like form. On the Pacific Coast of America there are two species, both large trees, valued for their timber. In eastern United States, C. Thujoides is locally known as "white cedar." C. nookatensis, the yellow or "canoe cedar," grows in the coastal forests of Alaska and British Columbia, extending southward to Oregon. It closely resembles in habit the giant Arbor vitae. C. Lawsoniana, the Lawson cypress or "Port Orford Cedar," is found in Oregon and northern California. It is a very beautiful tree, often seen in cultivation. Its timber is highly prized.

SECTION III. JUNIPEROIDEAE

Like the Cupressoideae the Juniperoideae are exclusively boreal. *Juniperus* is by far the most widespread of the Cupressaceae, and includes some sixty species, thus outnumbering all the other Cupressaceae. Species of *Juniperus* are found practically throughout the Northern Hemisphere, from the Arctic regions to Northern Africa and Central America. They are mostly shrubs or trees of small size. The red cedar, *J. virginiana*, may occasionally become a tree 50 feet or more in height. In western United States the traveler passing through the Great Basin sees many junipers (*J. utahensis*) on the barren hillsides; and in the higher mountains of the coast *J. occidentalis* is a picturesque feature of the exposed mountain summits.

The female flowers differ much from those of the other Coniferales. They are borne at the end of a short branch and consist of several whorls of sterile scales. The ovules may be borne directly at the apex of the shoot—sometimes a single one, sometimes a group of three alternating with a whorl of sterile bracts below them. In other cases one or more of the pairs or whorls of scales may be fertile, bearing one or two ovules.

The scales below the ovules become completely grown together enclosing the ovules, and as the seeds develop the tissue of enveloping scales becomes pulpy and sugar is present so that the ripe fruit cone resembles a globular berry.

PHYLOGENY OF THE CONIFERALES

The origin and relationships of the Coniferales have been the subject of innumerable publications for over a century and there is still no general agreement concerning these fundamental problems. Although there is no question that the ancestors of the conifers existed in the Palaeozoic, the fossil record is very fragmentary, and the relations of the oldest known fossil conifers to Palaeozoic seed plants and to the living Coniferales are very obscure.

So far as the geological evidence goes it seems probable that the Araucariaceae are the oldest. Kräusel believes that there is evidence for their existence in the Permian, while both *Agathis* and *Araucaria* were widespread during the *Jurassic*. It is probable that the other families also were represented during the latter period.

Most of the existing genera occur in the Cretaceous, and several—e.g., Sequoia, Phyllocladus, and Taxus—have been found in Jurassic formations, while Sciadopitys and probably Taxus are reported from the Rhaetic. The Pinaceae are represented in the Lower Cretaceous and probably existed during the Jurassic. Cedrus and Picea are recorded from the Lower Cretaceous, and in the Middle Cretaceous are forms intermediate between Cedrus and Pinus.

Owing to the rare occurrence of recognizable fruiting material of conifers from the Early Mesozoic, the great mass of work upon these has been restricted to a study of the vegetative structures. As the tissues, especially the fibro-vascular bundles, are often very well preserved, the value of these as a clue to relationships has been sometimes overstressed.

One theory of the ovule considers the ovulate cone to represent a single "flower," i.e., to be an aggregation of carpellary scales. Opposed to this is the view that the cone is an inflorescence made up of numerous simple "flowers," something like the catkins of a willow or poplar, each flower representing a shoot borne in the axil of a leaf. Each theory has arguments in its favor, but each also meets with difficulties in bringing all types into harmony with it. One of the latest contributions to the subject is that of O. Hagerup. On the basis of developmental studies made on a number of genera he concludes that, except for the Taxaceae and some of the Cupressaceae, the cone is an inflorescence. Lotsy has tried to solve this problem by dividing the Coniferales into two categories—"Florales" and "Inflorescentiales."

The various theories as to the nature of the cone in the Coniferales have been very completely reviewed by Pilger in his treatment of the Coniferales in the Natürlichen Pflanzenfamilien. His conclusion is that the evidence indicates that the cone is a single flower, i.e., the ovulate scales are simple sporophylls. The various modifications, like the "ovular scale" of the

Pinaceae and the epimatium of the Podocarpaceae, are regarded as outgrowths of the sporophyll and are structures concerned with the protection and nutrition of the ovules. Thus in the Pinaceae the closely imbricated ovular scales protect the developing ovules, and in such species as *P. radiata* the outer margin of the scale is expanded into a thickened "apophysis," so that the scales fit closely together and the seeds are completely enclosed. This is also the case in *Cupressus*; and in *Juniperus* the seeds are completely embedded in the pulpy "fruit." Thus the term "gymnosperm" is not entirely appropriate for all the conifers.

In Araucaria the cone is composed of scales, upon which the ovule is situated very much as the sporangium of the Lycopodineae is placed upon the sporophyll, and there is no trace of the subtending bract found in most of the Pinaceae. Pilger thinks this condition primitive and that of the

Pinaceae secondary.

The male flowers of the conifers are more uniform in structure than the female cones and it is generally agreed that the staminate strobilus is a single flower. There are, however, certain differences within the order. In the Taxaceae (especially Taxus) the pollen sacs are coherent and form a sort of synangium, which might be compared to the anther of the angiosperms. In the Cupressaceae the free pollen sacs are borne on the abaxial surface of the expanded tip of the stamen, while in Araucaria the numerous slender pollen sacs are pendent. In the Pinaceae there are but two sporangia, coherent with the abaxial surface of the stamen.

Pilger believes that the existing families are phylogenetically farther apart than is generally assumed and are not to be considered as derived one from another. He concludes that they are the ends of separate phyla

derived from some very remote group of common ancestors.

The Taxaceae are especially difficult to bring into line with the other Coniferales, and it has been proposed to place them in a separate order, apart from the other conifers. The most natural conclusion from a study of the ovule of Taxus is that it really arises independently from the apex of a shoot and that there is no carpellary leaf present. Pilger's conclusion of its cauline origin is confirmed by observations made by the writer, and the suggestion to remove the Taxaceae from their association with the Coniferales seems justified.

The relation of the Coniferales to the Palaeozoic pteridophytes and seed plants is very uncertain. The obvious similarity in habit of the conifers and the Lycopodineae is sufficiently familiar, and a direct relationship of the living conifers with the Palaeozoic arborescent lycopods, like Lepidodendron, has been suggested. Seward, in his studies on the Araucariaceae, reached this conclusion, and recently several investigators—e.g., Kierstein, Mez, Hagerup—have adopted this theory. The first two base

their conclusions upon the serum-diagnostic theory; but Hagerup made a comparative anatomical study of the two types. He suggests the following succession of forms: Psilophyta, Selaginellaceae, Lepidospermae, Cordaitales, Coniferales.

Wettstein, Zimmermann, and others believe the whole series of gymnosperms are "Pteropsida," i.e., are derived from fern-like ancestors, and that the similarities between Lycopodineae and Coniferales are a parallel development—homoplastic—and do not indicate any genetic relationship. Zimmermann, discussing the interrelationships of the Coniferales, favors the classification of Wettstein, who makes three main divisions (orders?): Taxaceae, including Podocarpaceae and Cephalotaxaceae; Abietaceae, viz., Araucariaceae and Pinaceae; and Cupressaceae, with Taxodiaceae and Cupressaceae.

Pilger's final conclusion is that among the gymnosperms several independent phyla should be recognized whose relationships with the pteridophytes, in a wide sense, are very uncertain. The cycadophytes are certainly related to the Filicineae. The Bennettitales and Cordaitales are independent phyla; a connection of *Araucaria* with the latter is quite impossible, owing to fundamental differences in the flowers. Whether the Ginkgoales are most nearly related to cycads or to the conifers is uncertain, and a direct connection of conifers and Lycopodineae is at least doubtful. Taxaceae, on one hand, and Araucariaceae, on the other, diverge most widely from the typical Coniferales.

CHAPTER XXII

GYMNOSPERMS—GNETALES

The order Gnetales includes three genera which differ much from each other. These genera, *Gnetum*, *Ephedra*, and *Welwitschia*, have generally been referred to a single family, Gnetaceae; but the more recent studies of the order, e.g., that of Markgraf in *Die Natürlichen Pflanzenjamilien*, make each genus the type of a family.

The relationships of the Gnetales with the Coniferales, on the one hand and with the angiosperms on the other have been widely discussed but are very problematical; and as their geological history is practically unknown, their systematic position must for the present remain very doubtful. It is generally admitted, in spite of the absence of fossil evidence, that the Gnetales are very old types and that the three living genera may represent the end members of divergent phyla from some remote, possibly common, ancestors. Their present distribution also indicates their ancient origin.

While the three genera differ much in many respects, they have certain points in common which distinguish them from the other gymnosperms. The flowers are provided with protective envelopes, recalling the perianth of the angiosperms; and the ovules and stamens also have been compared with those of the angiosperms. The opposite leaves, especially those of Gnetum, are strikingly like those of many dicotyledons; and the vascular bundles have true vessels, a character common in angiosperms but very rarely found in the gymnosperms. Because of these characters they have been considered by many observers as possibly directly related to some of the lower angiosperms.

CLASSIFICATION

FAMILY 1. EPHEDRACEAE

Of the three genera, *Ephedra* is probably the most primitive. There are about thirty-five species (Markgraf) which have a very wide geographical distribution. Four species are found in the arid regions of the United States, and others in Mexico and in South America as far south as Patagonia.

The American species are low branching shrubs, with decussate leaves reduced to dry pointed scales united into sheaths about the nodes of the

shoots, which resemble the slender sterile branches of Equisetum. The young branches have abundant chlorophyll. There is a tap root which persists for a long time, but later, lateral roots are formed from the base of the stem. The slender green shoots are shed periodically; but the main branches develop cambium, and a secondary thickening like that in the conifers is formed but is only slightly developed. The leaf scales may sometimes be in threes or fours. The surface of the shoot is marked by parallel furrows, as in Equisetum, and stomata occur on the sides of these.

The wood is composed in part of tracheids with bordered pits, much like those of the conifers, especially the Araucariaceae. Associated with the tracheids are vessels also showing bordered pits. The transverse walls

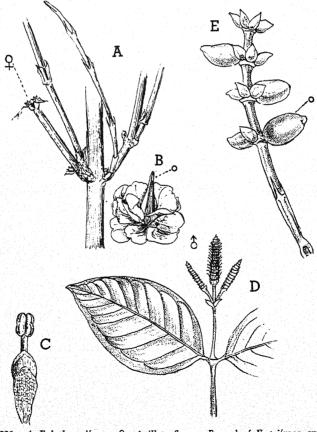


Fig. 286.—A, Ephedra trifurca; Q, pistillate flower; B, seed of E. trifurca, surrounded by many scale leaves; C, staminate flower of E. altissima; D, Gnetum latifolium; c, staminate inflorescence; E, young fruits of G. gnemon (C, D, after Eichler, from Engler and Prantl; E, after Lotsy).

in the vessels are only partially absorbed—a condition intermediate between the coniferous tracheids and the true vessels of the angiosperms.

Leaves.—The thin scale leaves are composed of only a few cell layers. There is a single layer of palisade cells below the epidermis, which develops stomata. A small amount of mesophyll surrounds the two vascular bundles of each leaf. The greater part of the green tissue is in the cortex of the shoot.

Flowers.—The species of Ephedra are typically dioecious, but exceptionally the staminate and ovulate flowers may occur on the same plant or even in the same strobilus. The strobilus is composed of several pairs of decussate scales—the lower ones sterile and each fertile one having a flower in its axil. The strobili are formed at the nodes of the slender green branches.

The staminate strobilus consists of an axis, bearing the scales. Sometimes secondary strobili develop from the base of the strobilus. In the axil of each fertile scale is the very simple staminate flower which consists of an elongated sporangiophore having several pollen sacs at its summit. Enclosing the base of the sporangiophore are two opposite bracts which have been compared to the perianth of the angiospermous flower. The pollen sacs are united into a synangium, which is usually bilocular but may be trilocular or even quadrilocular.

The nature of the sporangiophore is not entirely clear. Coulter and Chamberlain state that it is an axial structure which seems pretty evident. This seems to be much more likely than the view of several other observers (e.g., Thoday, Arber, and Parkin) that it is a foliar structure, sporophyll. In view of the fact that similar sporangiophores are found in the most primitive seed plants and that foliose sporophylls are presumably secondary, it would seem most likely that the sporangiophore in *Ephedra* is the retention of a very primitive organ—which is also probably true of the stamens of the angiosperms—rather than a structure derived from some ancestor with foliaceous sporophylls.

It has been suggested that the Gnetales and Bennettitales have come from a common stock; and if this is true one might compare the sporangiophore in *Ephedra* with that of the simpler Bennettitales, like *Williamsoniella*, rather than with the elaborate pinnate sporophylls of the specialized Cycadeoideae.

The ovulate strobilus is composed of several pairs of sterile scales (bracts); and the solitary ovule, usually only one ovule being developed, is apparently derived from the apex of the axis. Sometimes, e.g., E. distachya, there are two ovules which Thoday states are formed in the axils of the upper pair of bracts and not directly from the shoot apex. It is stated that in certain species with trimerous bracts there may be three ovules.

The development of the ovule has been studied by Land in the American E. trifurca. The ovule is surrounded by two bracts, forming a rudimentary perianth like that of the male flower. The ovule has two distinct integuments, the inner one greatly prolonged beyond the apex of the nucellus and forming a narrow micropylar tube which secretes a drop of fluid at the apex. A conspicuous pollen chamber is present.

As the seeds develop, the scales of the strobilus may become concrescent and fleshy in texture; in *E. trifurca* and other species they remain free but increase in size, forming loose chaffy scales.

The gametophytes.—Land has made a very complete study of the development of the gametophytes in *Ephedra trifurca*. The first division in the pollen spore takes place before it is full grown and separates a small prothallial cell from a very much larger one. The nucleus of the large cell divides next into two of unequal size, the smaller one representing a second prothallial cell, the larger one the antheridium mother cell. The mature pollen spore has five nuclei, representing two prothallial cells, stalk and body cells, and the tube nucleus.

The development of the female gametophyte is very much like that of

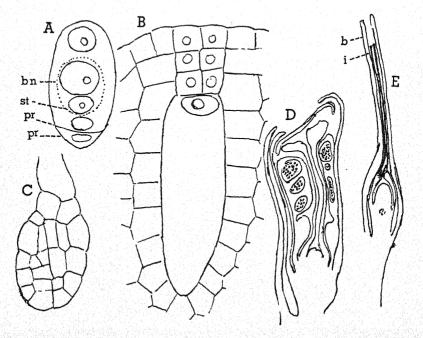


Fig. 287.—A, male gametophyte of Ephedra trifurca; pr, prothallial cell; bn, body cell; st, stalk cell; B, archegonium; C, young embryo; D, staminate flower of Welwitschia; E, pistillate flower of same (A-C, after Land; D, E, after Chamberlain).

the typical conifers. The young ovule shows a single megaspore mother cell, which divides transversely into four megaspores, the lower one developing into the embryo sac. The numerous free nuclei are embedded in the parietal cytoplasm, approximately 256 free nuclei being formed before the first cell walls appear.

The growth of the endosperm is rapid, and there is a differentiation of the tissue into a micropylar and antipodal region. The archegonia are formed from the micropylar tissue.

The archegonium, like that of the Coniferales, has a large central cell and a primary neck cell. The latter divides repeatedly, and a conspicuous neck is formed, composed of four rows of neck cells, which may become less definite owing to later irregular divisions. A ventral canal cell nucleus is formed, but there is no cell wall separating it from the egg cell.

Fertilization.—Within ten hours after the pollen spores are deposited in the drop of fluid at the apex of the micropylar tube, fertilization may be completed.

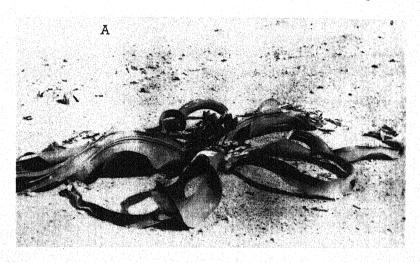
Embryo.—The fusion nucleus divides until 8 free nuclei are formed, thus resembling many conifers; but instead of forming a single proembryo, each nucleus forms about itself a cell wall and there are thus 8 free cells embedded in the endosperm. The largest of these cells—usually 3–5—develop suspensors bearing an embryo. During the growth of the proembryo the walls of the mantle cells surrounding the egg cell break down and the contents migrate into the egg, where they closely resemble the proembryo cells derived from the fusion of the gametes. The suspensor elongates and pushes the young embryo into the endosperm. With the growth of the embryo a secondary suspensor is formed and the primary suspensor collapses. Although several embryos are formed, only one reaches maturity. The embryo sporophyte is dicotyledonous.

FAMILY 2. WELWITSCHIACEAE

Welwitschia mirabilis, the only species, is one of the most remarkable plants known to the botanist. It is restricted to the arid coastal region of southwestern Africa, within reach of the heavy ocean fogs, a condition comparable in a way to the range of the redwood and some other conifers in California. The plant body is a short massive trunk, only a foot or so in height but sometimes with the expanded "crown" a meter in diameter. The upper surface of the trunk or crown is concave and is divided into two lobes. Around the margin of the lobes is a deep groove, from which arise two enormous strap-shaped leaves, sometimes two or three meters long, and lying upon the ground. These leaves are the first ones that succeed the cotyledons and persist throughout the life of the plant, continuing to increase in length through the activity of a meristem tissue at their base.

A thick taproot penetrating to a great depth in the earth anchors the plant securely, and is believed to reach the water table in the excessively arid country where it grows. The trunk is often almost completely buried in the earth except for the crown, and below the insertion of the leaves has the form of an inverted cone; it has been called the stock. The whole has been compared in form to a turnip. The leaves in old plants become split into several ribbon-shaped strips, the tips being gradually worn away.

The seedling has a somewhat enlarged "hypocotyl," which merges into



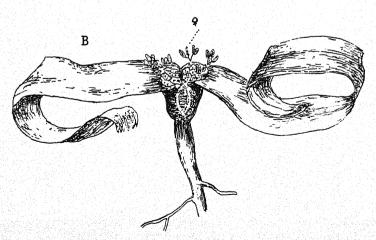


Fig. 288.—A, Welwitschia mirabilis (photograph by Dr. W. A. Cannon); B, somewhat schematic figure of mature plant; \mathfrak{P} , ovulate inflorescence (B, after Eichler).

the slender taproot. The two spatulate cotyledons are soon followed by the two permanent leaves which are at right angles to them. The leaves have parallel veins. In the axils of the cotyledons are formed buds, which later fuse and form the "crown" at the summit of the stock which is derived from the hypocotyl.

The two lobes of the crown show a series of concentric ridges, marking periodic growing seasons, which, however, probably occur at very irregular intervals. These ridges arise from the activity of the meristem within the groove between the leaf bases and the margin of the crown. Upon these

ridges the inflorescences are borne.

The root of the seedling is diarch, with alternating xylem and phloem masses. There is a gradual transition from this condition to that in the hypocotyl, where there are four main collateral bundles. Higher up there are, in addition, numerous small bundles.

In the tracheary tissue spiral or annular thickenings predominate. In the secondary wood the tracheids may have bordered pits with reticulate thickening between. True vessels occur also in the secondary wood. A remarkable feature is the abundance of large spicular cells, lignified externally and incrusted with calcium oxalate crystals. The inner wall is of cellulose. Mucilage ducts, like those of the cycads, are present in various parts of the plant.

The leaves have a very thick epidermis, with the stomata more abundant on the upper side. Palisade tissue occurs both above and below, and

there are numerous thick-walled fibers.

Flowers.—Welwitschia is dioecious, the flowers forming conspicuous branching inflorescences which are borne at the ridge developed from the meristem in the groove at the base of the leaves. The individual flowers are in the axils of conspicuous bracts arranged in four series and form a distinct cone like that in the typical conifers. The bracts are bright red at maturity, and there is some evidence that the flowers may secrete nectar, thus suggesting the possibility of insect pollination.

The staminate flower consists of two pairs of bracts, forming the perianth, within which are six stamens, in two groups of three. They are borne on a margin of a tubular body within which is an abortive ovule. The stamen consists of a stalk (filament) and a trilocular synangium (anther). The abortive ovule has the integument extended into a pistil-like tube, terminated by a saucer-shaped body, the whole recalling the style and stigma of an angiospermous flower. The nucellus of the ovule is present, but no embryo sac is developed.

The presence of this abortive ovule in the staminate flower may indicate that the ancestor of *Welwitschia* had bisporangiate flowers, like the Bennettitales.

The female flower, according to Chamberlain, consists of only two broad perianth scales instead of the four of the staminate flower. These are united at their edges and enclose the ovule, which has a single integument, extending to form a long tube, which does not have the stigma-like structure found in the abortive ovule of the staminate flower. In the seed the flattened perianth scales become membranaceous wings. Pearson regards the "perianth" scales as an outer integument.

The gametophyte.—The pollen spore when discharged from the pollen sac has three nuclei, probably representing, respectively, prothallial, generative, and tube nuclei. In this condition the pollen spore reaches the apex of the micropylar tube of the ovule and finally reaches the apex of the nuclellus. Except for the formation of a prothallial cell, the development of the male gametophyte in Welwitschia is practically the same as in the typical angiosperms.

The development of the embryo sac is imperfectly known. From Pearson's investigations it seems probable that but one functional embryo sac is developed. From the repeated division of the primary nucleus there results a very large number (approximately 1,024) free nuclei. The majority of these are situated in the broad antipodal part of the embryo sac. Cell walls then are formed, dividing the embryo sac into large multinucleate cells.

Embryo.—The zygote elongates and divides into two cells—there are no free nuclei. The upper cell becomes the primary suspensor, the lower the proembryo. The older proembryo shows three superposed tiers of cells. The terminal tier forms a cap, and from this a group of inner cells gives rise to the definitive embryo. While numerous proembryos may be formed, only one as a rule becomes fully developed. The embryo in the ripe seed has two large cotyledons.

FAMILY 3. GNETACEAE

The Gnetaceae differ very greatly in habit from the other Gnetales. Ephedra and Welwitschia are pronounced xerophytes; but the species of Gnetum inhabit the moist tropics, especially in the Indo-Malayan regions. A smaller number are found in West Africa and the Amazonian region of America. The type species, G. gnemon, and a few related species are trees or shrubs; but the great majority of the thirty (about) species are climbers, some of them lianas of great size.

The stems are jointed and often are swollen at the nodes. The ample leaves are opposite and are like those of the typical dicotyledons. From the strong midrib the primary veins are pinnately arranged and branch near the margin of the leaf into a net of smaller veins. Between the main veins is a similar network.

The apical growth of the main shoots is unlimited, but from the joints of the shoot there are developed short branches which in the climbing

forms bear the foliage leaves. On similar shoots the reproductive organs are formed. These shoots arise in the axils of the leaves, which in the climbing species are reduced to scales at the nodes of the main branches.

The stem structure shows a good deal of difference in the arborescent and scandent species. In G. gnemon the structure of the stem is like that of the conifers or of Ephedra; i.e., there is a solid woody cylinder with permanent cambium. In the climbing species there are several concentric series of separate vascular bundles, similar in arrangement to Welwitschia and some cycads. There are numerous conspicuous vessels in the secondary wood, very much like those of the angiosperms. In the cortex are numerous mucilage ducts, fibers, and spicular cells like those in Welwitschia.

The anatomy of the leaf is much like that in many broad-leaved dicotyledons. There is a definite palisade layer below the upper epidermis and a spongy mesophyll. The midrib is traversed by 4–5 vascular bundles, which show a limited secondary growth. Mucilage ducts accompany the vascu-

lar bundles of the midrib.

Flowers.—The inflorescences are usually axillary but may be terminal on the small branches. Secondary lateral inflorescences may be formed at the base of the primary one, and there may be further development of such branches, so that for a long time new flowering shoots are formed from the same region.

Gnetum is normally dioecious, but sometimes ovules may be present in the staminate strobilus. Both male and female flowers are borne on slender, catkin-like structures. The slender axis of the strobilus has a series of cupshaped "cupules" composed of a circle of coalescent bracts. Within the cupule are the individual flowers, arranged in whorls. In the male inflorescence there are several whorls of staminate flowers in the axil of each cupule and above these is a whorl or crown of abortive ovulate flowers. In the male catkin the internodes are in most species short and the cupules close together. In the ovulate strobilus there is but a single whorl of flowers in each cupule, and the internodes of the axis are longer than in the male strobilus.

The male flower consists of a sheath (perianth) composed of two united bracts. This surrounds a cylindrical stalk (sporangiophore?), which has at its summit two diverging bilocular synangia opening by a median cleft. The whole is not very different from the male flower of Ephedra.

The fertile ovulate flower has the nucellus surrounded by three envelopes, the nature of which has been frequently discussed. They are sometimes considered to be all of them integuments. Other authorities regard the inner one only as a true integument and the two outer ones as constituting a perianth. Chamberlain believes that only the outer envelope is a perianth. The inner integument, as in *Ephedra*, develops an

elongated micropylar tube, and pollination, apparently, is much the same. The outer envelope, which is thicker than the others, has also been compared with the aril of *Taxus*.

After pollination the embryo sac in its growth destroys all of the nucellar tissue except a small amount at the apex of the nucellus. The inner integument remains as a thin membrane surrounding the remains of the nucellus and the embryo sac. From the second envelope the hard shell or testa of the seed is developed, and the outer envelope, which is more massive than the others, becomes the fleshy, bright-colored, outer portion of the berry-like ripe seed (or fruit?).

No prothallial cells have been observed in the pollen, and the first division separates the generative and tube nuclei. The generative nucleus divides into the stalk nucleus and the body cell, from which later the two gametes are formed.

The gametophyte.—The development of the gametophyte and fertilization are completed much more rapidly than in most gymnosperms and recall the conditions in many angiosperms. The development of the female gametophyte is best known in G. gnemon. The primary nucleus of the young embryo sac divides repeatedly until there are a large number of free nuclei, and these occupy a parietal layer of cytoplasm lining the greatly enlarged embryo sac. There is no cell formation until after fertilization has been effected. In other species there is no central vacuole. A number of the free nuclei in the micropylar region become invested with a cytoplasmic envelope and function as eggs-no trace of an archegonium is found. The male nuclei of the pollen tubes are discharged into the embryo sac and unite with the egg cells. As soon as fertilization has been effected there is a rapid formation of cellular endosperm, which completely fills the embryo sac. In the basal region the cells are more compact and may be compared with the antipodal cells of the angiosperm embryo sac, and the free egg cells are also reminiscent of the angiosperms. The development of the embryo is still very imperfectly known. Only the earlier stages are developed before the seed is detached. The zygote gives rise to several suspensors, which may branch, and at the apex of each suspensor a proembryo is formed. While in this condition the seed is detached and the further development proceeds as the seed germinates. The terminal cell of the suspensor (proembryo) gives rise to the definitive embryo. Thus numerous embryos begin to grow, but usually only one matures. The final germination of the seed is completed only after a long period. Nearly a year may elapse between the time the seed is shed and the appearance of the young plant above ground.

The older embryo has a large foot (haustorium) like that in Welwitschia. There are a long hypocotyl and two cotyledons.

RELATIONSHIPS

As practically no fossil Gnetales are known, any theories as to their origin must necessarily be largely speculative and their relationships with each other, and with other gymnosperms, are at present very problematical. The very specialized character of the few living species and their geographical distribution indicate that they are relicts of some ancient much more widely distributed group of plants from which were derived several phyla, of which the three living genera are the final members. With which of the main orders of gymnosperms, Cycadales, Coniferales, or Bennettitales the Gnetales are most nearly related, it is impossible to determine with any certainty, as each of these, in turn, has been proposed as most nearly related to the Gnetales.

Of the three genera, Ephedra, especially in its reproduction, is most like the Coniferales. Its female gametophyte is very similar in its development, and definite archegonia, not unlike those of the Pinaceae, are pressent. In the other genera no proper archegonia are present, and they have more in common with each other than with Ephedra. Ephedra, therefore, as regards the female gametophyte, probably is a more primitive form than Gnetum or Welwitschia. This applies also to the male gametophyte, which is more highly developed in Ephedra than in the other genera. The gametophyte of Welwitschia is to some extent intermediate between Ephedra and Gnetum. In most species of Gnetum the unfertilized embryo sac contains only free nuclei, a condition found also in the angiosperms. This, together with the floral structures, has led to much speculation as to possible relationships between Gnetales and angiosperms.

Arber and Parkin have assumed that the Gnetales and angiosperms are descendants of some bennettitalean ancestors. These hypothetical ancestors are supposed to have had a special floral type, "Proanthostrobilus," with both stamens and ovules. From some such ancestral forms it was believed that two parallel phyla developed, the angiosperms and Gnetales being the end members, respectively, of the two lines of evolution.

While this theory is not without considerable plausibility, it is based upon very meager data and there are many objections that can be offered. In his recent treatment of the Gnetales in Die Natürlichen Pflanzenfamilien, Markgraf gives a summary of his conclusions: "The Gnetales are gymnosperms whose ovules have a peculiar tubular integument (which is also found in some pteridosperms). In Ephedra there are archegonia like those of the conifers. Special features of the ovules and gametophyte recall special definite groups of gymnosperms—but the latter may be quite unrelated to each other. In such a completely isolated group as the Gnetales, one cannot distinguish between homologies and analogies, convergence and relationships. Consequently one can only say that the Gnetales exhibit

various primitive gymnospermous characters which are also encountered in other descendants of the 'Urgymnospermae.' That the Gnetales are ancient forms is certain; that is shown by their restriction to widely separated areas."

The reduction of the gametophyte, especially in Welwitschia and Gnetum, places them at the apex of the gymnosperms. The leaves of Gnetum and the dicotyledonous embryo also suggest relationship with the dicotyledons.

In spite of these similarities, Markgraf concludes: "There is never a complete agreement in structure, usually only an apparent similarity. Therefore we are driven to the conclusion to consider the Gnetales as the end members of a development in which the characters of the Gymnosperms reach a grade of organization comparable to that of the Angiosperms."

Lotsy concludes his treatment of the Gnetales as follows: "I still believe that the Gnetales represent the end of a developmental series which precludes the possibility of the Angiosperms being derived from them."

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CHAPTER XXIII

ANGIOSPERMS—ANTHOPHYTA

From the Permian through the Mesozoic to the Lower Cretaceous, the gymnosperms, represented at the present time by the cycads, Ginkgo, conifers, and Gnetales, were the predominant elements in the vegetation. From the Lower Cretaceous onward they diminish in importance and are to a great extent superseded by the angiosperms—Anthophyta, or "flowering plants," which form an overwhelming majority of the living species. While some gymnosperms, notably the conifers, are often important elements of the floras of many regions, owing to their gregarious habit, the total number of species of living gymnosperms is not much more than 500, compared with probably at least 150,000 described angiosperms, new species being continually added.

The angiosperms offer an extraordinary contrast to the gymnosperms in their marked adaptability, growing in every situation where plant life is possible. In size they range from almost microscopic aquatics, e.g., Wolfiella, to giant trees rivaling the largest conifers. A few forms even inhabit the sea, like the eelgrass (Zostera) and Phyllospadeix of the Pacific Coast. A considerable number, like the pondweeds, Naias, Potamogeton, Vallisneria, Ultricularia, and Nymphaea, are fresh-water aquatics. Others are marsh plants, including many rushes, sedges, and grasses, as well as a large number of semiaquatic species.

Contrasted with these aquatic and hydrophytic marsh plants are the xerophytic inhabitants of arid and semiarid regions where the water supply is precarious. These xerophytes are especially characteristic of the deserts, such as are found in southwestern United States and northern Mexico. The Cacti, the Agaves, the Yuccas, and many others are representative. These plants can endure extremes of heat and drought for long periods. Intermediate conditions of temperature and moisture, such as prevail in much of the Temperate Zone, are adapted to a very large number of species. In the tropics, especially where the competition for existence is particularly keen, there are many species of climbing plants and "epiphytes," such as many orchids, species of figs, rhododendrons, and, in America, the large family of bromeliads, of which the so-called Spanish moss is the most familiar. There are even true parasites like the dodder and the mistletoe, and saprophytes, like the Indian pipe (Monotropa), which have lost their chlorophyll and live like fungi on decaying vegetable matter. These are but a few examples of the protean angiosperms.

This adaptability is in strong contrast to the limitations of the gymnosperms. The latter are all woody plants, trees or shrubs, adapted to a much more restricted range of conditions for their growth. They have thus been unable to compete on equal terms with the much more adaptable angiosperms.

The angiosperms differ from the gymnosperms in having the ovules, and later the seeds, contained in a special structure, the ovary; but this is perhaps not a fundamental difference. In some of the gymnosperms the seeds may be completely enclosed in the coherent scales of the cone, so that one might say that an angiospermous fruit was the result. However, there are far more important differences that exist between angiosperms and any gymnosperms, and it is very doubtful if there is any except the most remote relationship existing between the two main divisions of the spermatophytes.

In attempting to connect the angiosperms with the gymnosperms it is the Gnetales and some types of Bennettitales that have been suggested as the possible progenitors of modern flowering plants. It has been pointed out that the evidence in both cases is very doubtful; and an independent origin of the angiosperms from generalized "protangiosperms," as proposed by Engler in his introduction to the angiosperms in the Natürlichen Pflanzenlamilien, seems more plausible.

Any attempt to explain the ancestry of the angiosperms is necessarily largely hypothetical and involves the much disputed question whether they are strictly monophyletic or whether there are several independent phyla, or at least separate lines of descent, extending farther back than can be shown by any record at present available. The assumption of a single primordial floral type of which all others are derivative still has some advocates, but it is likely that most recent students of floral evolution are inclined to favor a polyphyletic origin for the larger groups of angiosperms. This conclusion seems justified, both from a morphological study of living types and from the geological evidence.

A recent advocate of the monophyletic origin of the angiosperms is J. Hutchinson. He assumes that the primitive flower was "bisporangiate, apocarpous, with a petaloideous perianth," a type closely resembling the living Magnoliaceae and Ranunculaceae. From such a flower the much simpler flowers, for example, of the oak and willow families have been derived by reduction. Hutchinson's views were evidently influenced by Arber's papers on the origin of the angiosperms and also, perhaps, by earlier papers of Bessey and others who like Arber assumed a monophyletic origin for the angiosperms. The discoveries of the "flowers" of the Bennettitales, especially by Wieland of the wonderfully perfect petrified specimens of cycadeoids from the Mesozoic formations in Wyoming and South Dakota, invited a comparison with such flowers as Magnolia. Arber concluded that the cycadeoids were more nearly related to angio-

sperms than to the true cycads and that the cycadeoid flower was really homologous with the flower ("anthostrobilus") of the primitive angiosperms. He did not claim that the latter were derived immediately from the cycadeoids (Bennettitales), but that the two had developed from a common stock.

Much closer in appearance to the flowers of some of the simpler Polycarpicae (Ranales) are the older Bennettitales, Williamsoniella and Wielandiella. Unlike the cycadeoids of the Cretaceous, the habit of which was much like that of the true cycads, these forms had slender forking stems and small scattered leaves. Wieland believes that the dicotyledons may have come from forms like these and may have originated as far back as the Permian. He contends that the development of numerous nearly parallel stocks is much more likely than a dichotomizing common stock from comparatively recent ancestors. He also holds that many assumed homologous structures are really homoplastic.

Wettstein assumes a direct derivation of the angiosperms from gymnosperms, but instead of connecting them with the Bennettitales he sees in the Gnetales the nearest living relatives of the dicotyledons. The angiospermous flower is interpreted not as a strobilus ("anthostrobilus") but as an inflorescence comparable to that of the Gnetales. Wettstein believes that the primitive flower was monosporangiate, its perianth homologous with a circle of bracts, each subtending a stamen or an ovule, constituting

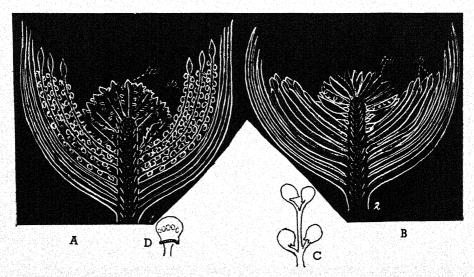


Fig. 289.—A, "proanthostrobilus" of a "hemi-angiosperm"; B, "anthostrobilus" of a primitive angiosperm; C, Gristhorpia Nathorsti, a Jurassic "angiosperm"; D, fruit of Caytonia Thomasi (A, B, after Arber & Parkin; C, D, after Hamshaw-Thomas).

a very simple flower. The stamens were bilocular, but by the fusion of two such primitive flowers would result a stamen with four loculi comparable to the staminate flower in *Ephedra*. The origin of the bisporangiate flower is explained by assuming the occurrence of ovulate flowers at the apex of a staminate inflorescence, resulting in a flower with terminal ovary and subtending stamens.

The assumption that the primitive angiosperms had flowers of the ranalian type, such as *Magnolia*, and that all other floral types are derivatives of this, is pure hypothesis and based almost entirely upon a comparison of existing species, for the most part ignoring the geological evidence, which

is by no means in accord with such an hypothesis.

That Magnoliaceae did exist in the Cretaceous is certain; but the earliest known angiosperms from the Lower Cretaceous are almost entirely apetalous genera, like *Populus* and *Ficus*, or monochlamydeae with inconspicuous and presumably wind-pollinated flowers. If these early types are descendants of petaloideous ancestors, some of the latter must have existed during the Jurassic; but as yet no such forms have been discovered and it is fair to conclude that that they did not exist. That entomophilous flowers could hardly have existed before the Cretaceous is indicated by what is known of the Jurassic insects (Handlirsch). The flower-haunting insects, bees, and butterflies seem to have been quite wanting. All the early fossil insects are primitive types, unfitted to pollinate flowers.

Engler in his introduction to the angiosperms has treated at some length their origin. He rejects Hutchinson's hypothesis of a derivation from Bennettitales and Wettstein's theory of a direct derivation from forms related to the Gnetales. Engler predicates the existence during the Mesozoic of an extensive complex of forms having many of the characters of the true angiosperms, which have originated from these "protangiosperms."

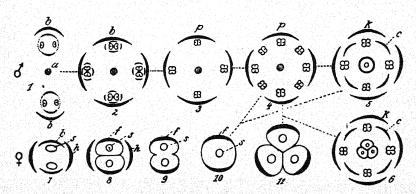


Fig. 290.—Diagram showing derivation of a bisporangiate flower from a gymnospermous (Gnetales) inflorescence (after Wettstein).

From the protangiosperms it is assumed that numerous independent phyla developed, some monocotyledons, others dicotyledons. Engler believes it very unlikely that any of the existing phyla are derived from any of the others, but the main groups or phyla of existing angiosperms are to be considered rather as parallel lines of evolution originating independently from protangiosperms. He suggests that a mutation in a single individual of a group might appear in a similar but not identical form in other individuals, thus perhaps giving rise to different races which would have much in common but could hardly be traced back to a common ancestral form.

The geological history of the angiosperms is very incomplete. In the Lower Cretaceous many fossils have been found, but nearly all of these are clearly related to living genera and are even referable to them; e.g., Ficus, Platanus, and Sassafras. It is evident that there must have been a long line of more primitive ancestral forms, presumably extending into the Jurassic; but as yet these have not been discovered. It has been suggested that perhaps remains of these ancestral forms may be found in some as yet unexplored tropical regions.

In this connection may be mentioned the discovery, by Professor Hamshaw-Thomas, in Jurassic rocks in England, of some remarkable fossils, the Caytoniales, which show fructifications that might be described as angiospermous but differ very greatly from any known existing angiosperms. The discovery of these Jurassic Caytoniales suggests that further investigation of rocks of similar age, especially in the tropical regions, may reveal still other angiospermous fossils.

THE FLOWER

The "typical" flower is commonly described as the equivalent of a leafy axis, with the various floral organs arranged like the leaves of a vegetative shoot. It is also frequently assumed that from this "typical" flower all the other floral types have been derived—a view which certainly is not consistent with our present knowledge of the development of floral structures.

The essential organs of the flower are the stamens and carpels—or perhaps better, the pollen sacs (microsporangia) and ovules (megasporangia). The stamens and carpels are often described as sporophylls, but it is now pretty well agreed that these sporophylls are not metamorphosed foliage leaves but organs, *sui generis*.

Both comparative morphology and the fossil record show that the sporangia are fundamental structures and not secondary developments of foliar origin. The first sporangia are found in the most primitive of the vascular plants before any definite leaves are developed. In the Psilophytales, many pteridosperms, and Cordaitales, as well as the more primitive ferns and

Equisetum, the sporangia are borne on special sporangiophores which are independent of any foliar structures. The microsporangia of the vascular plants have remained extraordinarily uniform in structure, and the pollen sacs of the angiosperms do not differ essentially from the sporangia of the primitive homosporous pteridophytes. The transference of the sporangia to the surface of the sporophylls in many ferns is probably a secondary condition, the more primitive types having marginal sporangia.

The stamen.—The stamen in most angiosperms consists of a stalk or filament, having at its apex the "anther." The latter is usually bilobed—each lobe representing a bilocular synangium. The filament may perhaps be interpreted as a sporangiophore. Among the living gymnosperms the stamens of Ginkgo are perhaps most like those of the angiosperms. There is also a certain resemblance to the stamens in the male flowers of Ephedra, but in both these examples the resemblances are probably homoplastic rather than homologous. The angiosperm flower may consist of a single stamen, but the number is in most cases much greater. The aggregate of the stamens is known as the "androecium."

The carpel.—Like the stamens, the number of carpels varies greatly, and not infrequently only a single carpel is present—the carpels together form the "gynoecium." Where several separate carpels are present, the

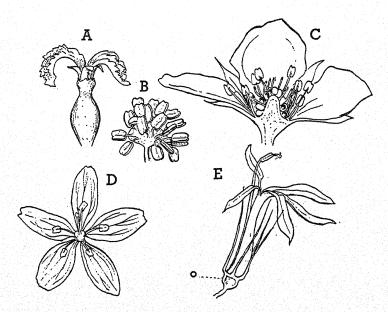


Fig. 291.—Types of angiospermous flower. A, pistillate flower of Juglans; B, staminate flower of Populus; C, flower of a strawberry; D, actinomorphic flower of Claytonia; E, zygomorphic flower of Lobelia.

flower is "apocarpous"; where they are coalescent it is "syncarpous." In the latter case the united carpels form a pistil. In the simple apocarpous type, the carpel suggests a folded leaf and has usually been thus interpreted, the ovules being attached to the coherent margins of the leaf. Some recent studies (Hamshaw-Thomas) on these forms, however, show that this explanation is not justified and the general interpretation of the carpels as sporophylls is open to question—although the nature of the carpels is not always clear, and the relation of the ovules to the carpels varies greatly. In a good many cases the ovule is developed directly from the apex of a shoot, or the latter may form a "placenta" bearing numerous ovules. More commonly, however, they are borne by the carpels. The carpels may be leaf-like in appearance, but it is doubtful if they are really homologous with the true leaves.

The pistil, whether composed of a single carpel or of several united ones, usually shows the three regions: the ovary at the base, containing the ovules; and the style—generally a more or less elongated tube, bearing at its apex the stigma, having a papillate or viscous surface which receives the pollen. The ovary may have a single cavity or may be divided in several chambers or loculi.

The prevalent view that such a simple follicle as that of many Ranunculaceae is the homologue of a simple folded leaf with the ovules borne on the infolded leaf margins is refuted by the investigation of *Caltha*, *Helleborus*, etc., by Hamshaw-Thomas, who showed that the veins of the valves of the follicle, instead of extending from the "midrib," are connected with two vascular bundles close to the margins of the valves and from these bundles, and not from the margins themselves, the ovules are developed.

Extensive studies of the carpel structures have been made by Miss E. R. Saunders. She concludes that the "monomorphic" theory, i.e., that all carpels are modifications of a common primordial type, is not valid, and claims that there are several fundamental types of carpels which are therefore "polymorphic," although she believes they are foliar structures. On this assumption it is held that several carpellary types have arisen in the evolution of the flower, with an accompanying separation and redistribution of the carpellary functions. These functions are, respectively, receptive, reproductive, and protective.

Three fundamental types of carpels are recognized, viz., valve, solid, and semisolid carpels. The valve carpel conforms most closely to the theoretical "folded leaf" theory. It shows a "midrib" and pinnate venation. This structure, however, is refuted by Hamshaw-Thomas's investigations. Two types may occur in the same flower and represent two series, such as often occurs in the stamens.

The solid carpel may be greatly reduced and more or less intimately

fused with its neighbors. The presence of such solid carpels has not been

recognized generally.

The semisolid or pseudovalve carpel resembles in form the valve carpel but has the placentae displaced from the contact edges of the carpels. In the typical apocarpous valve carpel, like that of many Ranunculaceae, the style and single stigma are developed from the apex of the carpel and the placenta bears two rows of ovules corresponding to the two parallel vascular bundles marking the united margins of the carpel.

In its most developed form the solid carpels are distinct and may extend into the cavity of the ovary, forming so-called false septa—as in Capsella and some other Cruciferae. Miss Saunders considers that in this case there are four carpels—two valve carpels and two solid ones—instead of the usual view that there are only two carpels. The semisolid or pseudovalve carpel has the appearance of a true valve but differs in having the placentae displaced from the contact edges of the carpels to a position on either side of the center line.

In the Liliaceae, which are generally supposed to have three carpels, according to Miss Saunders there are six, corresponding to the number of the perianths and stamens. In the Leguminosae, which are generally supposed to have only a single carpel, Miss Saunders recognized two and in some cases more.

Flowers may be bisporangiate, having both stamens and carpels, or they may be monosporangiate—borne on different plants, which are thus "dioecious"—or on different parts of the same individual, when the plant is "monoecious." As examples of familiar monoecious plants may be mentioned: Indian corn, calla lily, oak, and walnut. Poplar, willow, and date palm are representative dioecious forms. The bisporangiate flowers are often called "perfect," or "hermaphrodite."

In most of the flowers, in addition to the stamens or carpels, there is a "perianth" composed of more or less modified, leaf-like organs. In the more primitive flowers there may be only a single series of perianth leaves. Such flowers are "monochlamydeous." Where there are two series of perianth members they are "dialypetalous." In the latter case the outer perianth leaves, the sepals, are very generally green and are undoubtedly true leaves. The inner perianth, the corolla, usually is made up of very delicate, conspicuously colored petals, which there is good reason to believe are modified stamens and not true leaves. The development of the showy corolla is, of course, associated with the entomophilous habit of so many angiosperms, and it is by no means unlikely that the development of a true corolla was preceded by the development of showy stamens such as are still characteristic of such genera as Salix, Thalictrum, Acacia, Eucalyptus, and other Myrtaceae. All of these belong to families which are recognized

as relatively primitive ones. In these the corolla is either entirely absent or relatively inconspicuous. The change of stamens into petaloid organs, or "staminodia," can be seen in *Canna* and *Mesembryanthemum* and many double cultivated flowers. A familiar case of the transition from stamens to petals is that of the water lily.

Where the perianth is monochlamydeous the segments (sepals) may become petaloideous, e.g., *Anemone, Clematis*, and *Daphne*. In most monocotyledons, although there are two series of perianth leaves, they are usually both petaloid, e.g., lily, *Amaryllis*.

It is generally admitted that the apocarpous flowers with indefinite number of parts are more primitive than those in which the parts are definite in number. We might compare the flower of Magnolia or Anemone

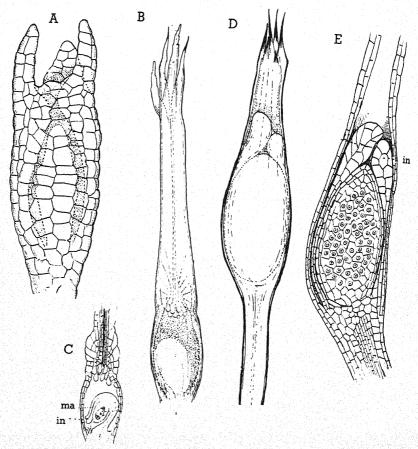


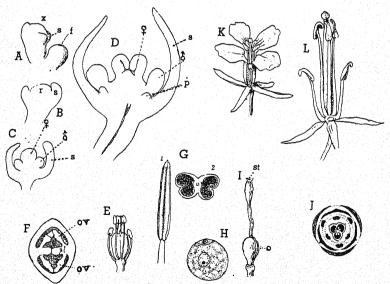
Fig. 292.—Naias flexilis. A, young, B, mature pistillate flower; C, section of pistil, showing solitary basal ovules; D, mature stamen; E, section of young stamen; in, integument.

with the more specialized flower of a geranium or lily. Specialization tends to a reduction in number of parts and cohesion of the organs. In such highly specialized flowers as *Iris* or *Campanula*, the petals are united into a tube and the ovary is fused with the base of the flower.

The arrangement of the floral organs may be either spiral or cyclic. The spiral arrangement is generally regarded as the more primitive, but both may occur in the same flower.

The modifications of the angiospermous flowers are far too numerous to be treated at length and a few representative examples must suffice. The simplest form which the flower can assume may be represented by Naias flexilis. It consists of a carpel with a single ovule or a stamen with a single pollen sac. In their earliest stages the two flowers are identical in appearance. Both ovule and stamen arise from the apex of the floral axis and each is enclosed in a sheath, which in the ovule has been interpreted as a carpel. In both stamen and ovule there is in addition a definite integument. The outer envelope of the stamen resembles closely the carpellary envelope of the ovule. The resemblance of the young stamen and ovule to the sporangia of certain pteridophytes, especially Azolla, where there is a similar "integument" about the megasporangium, is noteworthy.

There has been some controversy as to the nature of the outer envelope



in *Naias*, which has been explained variously as a carpel, a perianth, or merely a bract. Whether the extreme simplicity of the flower of *Naias* and the remarkable similarity between its ovule and its stamen indicate a primitive condition or a reduced one it is impossible to determine.

In a simple bisporangiate flower with all the parts present, i.e., sepals, petals, stamens, and carpels, these organs are attached to the apex of a special shoot, the floral axis, whose further growth is thus terminated. As a rule the sepals are first differentiated, followed by the stamens, the petals not infrequently first becoming evident at a later stage. The ovary may begin as a ring-shaped wall surrounding the apex of the shoot, or separate carpels may be formed independently. These later unite to form the closed ovary, tipped with the style and the stigma. The number and position of the ovules differ greatly.

In the majority of the angiosperms the stamens show a definite filament and two-lobed anther, the lobes separated by an intermediate mass of tissue, the "connective." There are, however, many modifications. Thus in *Ricinus* there is a much-branched sporangiophore, the ultimate branches bearing the anthers. In the Malvaceae the branching sporangiophores are united at the base into a tube. The development of petal-like staminodia has already been referred to.

The early development of the anther is much like that of the synangium of the Marattiaceae. It is at first composed of a mass of uniform tissue, except for a definite epidermal layer. The two-lobed form is soon evident, and in each lobe the two masses (loculi) of sporogenous tissue become segregated. These arise from a definite layer of hypodermal cells, very much as in the synangium of *Marattia* or *Danaea*. Between the sporogenous tissue and the epidermis several layers of cells are formed by a series of periclinal divisions. The innermost of the cells develop the tapetum, the outer ones contribute to the wall of the anther. The layers of wall cells next to the epidermis usually develop on their walls spiral bands like those in the pollen sacs of some gymnosperms and the sporangia of *Equisetum*. This layer of cells is the "endothecium." While the endothecium usually consists of a single layer, it may sometimes have several.

The tapetal cells may become multinucleate, and finally, together with the inner parietal cells, become disorganized as the development of the sporogenous tissue proceeds. As the pollen spores mature, only the epidermis and the endothecial cells remain intact.

The most marked departure from the typical stamen is found in *Naias*, where the stamen is formed directly from the shoot apex and the sporogenous tissue is developed from the central tissue (plerome) of the stem apex; and in *N. flexilis* only a single mass of spores is formed.

Pollen.—The development of the pollen spores of the angiosperms is essentially the same as those of the gymnosperms or the spores of the pteridophytes. The spore mother cells usually separate before the first nuclear division. This first division is a reduction division and establishes the haploid chromosome number in the spores. The pollen spores most commonly show the tetrahedral arrangement. Sometimes the meiotic division is followed by a division wall and the second nuclear division is similar, so that the four young spores form quadrants of a sphere. This type, the "bilateral" type of pollen, is common in many monocotyledons.

Except in some aquatic species the pollen spore shows a thick outer wall, like that in the spores of the ferns and liverworts. Like these there is an outer cutinized "exine" and an inner cellulose layer, the "intine."

The pollen spores usually become completely separated; but there are numerous exceptions, especially among the orchids, where they remain together, forming in many cases special pollinia, or pollen masses. Somewhat similar pollinia occur in the milkweeds (Asclepias).

Like the gymnosperms the pollen of the angiosperms begins to germi-

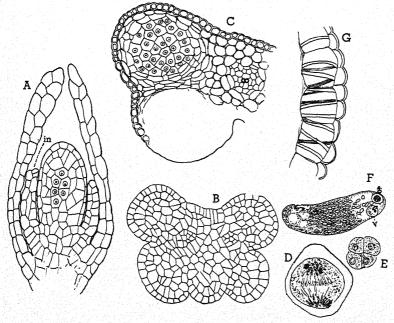


Fig. 294.—A, young stamen of Naias flexilis; in, integument; B, section of young stamen of Lilaea subulata; C, an older stage showing sporogenous tissue; D, first division in the pollen mother cell of Allium canadense; E, young pollen tetrad of Naias flexilis; F, ripe pollen spore of Naias; c, generative cell; G, cells from the anther wall of Lilaea.

nate within the microsporangium. The first division results in a small generative cell cut off from the body of the spore. There may be a definite division wall, e.g., Naias; or the generative nucleus, enclosed in a mass of cytoplasm, may be free in the spore cavity. The generative nucleus may divide into the two male gametes before the spore is shed, or this division may be delayed until the pollen tube is formed. As a rule, no prothallial cells are formed; but in exceptional cases, e.g., Sparganium simplex, a small cell is cut off before the generative nucleus has been formed.

The ovule.—The ovule of the angiosperms in most cases differs very little from that of the Coniferales in its general characters, except that as a rule a second integument is present; but there are many exceptions. There is very generally a definite stalk or "funiculus," and the ovule may be quite erect and symmetrical (orthotropous) or may be bent over (anatropous). Much less often it is campylotropus—bent in the middle. In a good many of the more primitive angiosperms, e.g., Naias, Peperomia, Polygonum, and Juglans, the ovule is cauline, i.e., developed from the apex of a shoot.

In longitudinal section the nucellus of Naias shows the same arrangement of the tissues as the vegetative shoot, i.e., a superficial layer, the

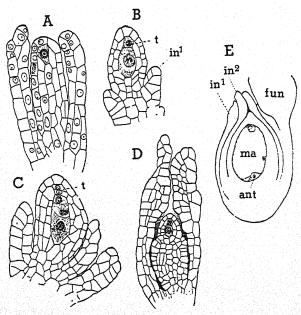


Fig. 295.—A-D, development of the ovule in Naias flexilis; t, tapetum; E, section of mature ovule of Sparganium simplex; ma, embryo sac; in¹, in², integuments; fun, funiculus; ant, antipodal cells.

"dermatogen"; a hypodermal layer, "periblem"; and a slender central cylinder, the "plerome." Like the stamen, the ovule develops a single integument. The archesporium originates from a single hypodermal cell, which divides by a periclinal wall into an outer tapetal cell and an inner one, which divides into two, sometimes three, cells. In most angiosperms the ovule is borne on the placenta developed from the carpels.

Embryo sac.—The development of the embryo sac has been followed in many angiosperms and in most of them there is great uniformity. There are, however, a number of marked departures from the type. In what is regarded as the normal type, the inner of the two cells resulting from the division of the primary archesporial cell is considered to represent the megaspore mother cell. This divides into four daughter cells like that in Pinus. The first division is the reduction division and the four resulting "spores" are haploid. It often happens, however, that the primary sporogenous cell (mother cell) becomes at once the young embryo sac, or even no tapetal cell may be cut off and the primary archesporial cell becomes at once the embryo sac. It is evident that in such cases the embryo sac cannot be strictly considered to be the homologue of a megaspore, and one might even question the assumption that the series of four cells resulting from the division of the inner of the two archesporial cells should be regarded as quite the equivalent of the megaspores of the heterosporous pteridophytes. The variation in the period when the reduction division takes place shows that the embryo sac can hardly be considered as the exact homologue of a megaspore. In Lilium, for example, the nucleus of the young embryo sac is diploid and the reduction divisions are completed within the embryo sac, resulting in the four haploid nuclei. The embryo sac in Lilium and many other similar cases should rather be compared with a spore mother cell than with a haploid megaspore.

However, whether the embryo sac is derived from one of the four haploid cells resulting from the division of the primary archesporium or later becomes at once the embryo sac, the further development proceeds in most cases in the same way and gives rise to the female gametophyte. If we must regard the four haploid nuclei in the young embryo sac of *Lilium* as representing four megaspores, we must assume that the gametophyte is the product of four megaspores—which seems hardly reasonable.

Atkinson, whose conclusions have not, perhaps, received as much attention as they deserve, believes that the embryo sac is not a spore comparable to that of the pteridophytes, or the pollen spores, but arises directly from the tissue of the nucellus, or from the archesporium without the intervention of true spores. He concludes: "It is to be interpreted as one adaptation of the plant in developmental processes under the influence of the changed and peculiar environment of the gametophyte which has be-

come so general in the angiosperms and probably in the gymnosperms." Atkinson's view seems to the writer the most plausible explanation of the great variability in the origin of the embryo sac in the angiosperms.

THE FEMALE GAMETOPHYTE

In most angiosperms the two nuclei resulting from the division of the primary nucleus of the embryo sac separate, one moving to the upper (micropylar) end of the embryo sac, the other to the lower (antipodal) region. Each of these undergoes two divisions and one nucleus from each group moves to the center of the sac. The three micropylar nuclei form the "egg apparatus," the lower the antipodal cells.

The nature of the cells of the egg apparatus is not entirely clear. The three cells have only plasma membranes and cannot well be interpreted as an archegonium, and possibly the three cells represent three free potential egg cells such as occur in *Gnetum*. One of these, the egg cell, usually lies below the other two, the "synergids." The antipodal cells very

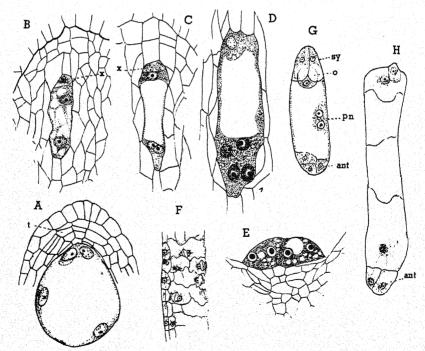


Fig. 296.—A, embryo sac of Peperomia pellucida; B-D, early stages in development of embryo sac in Pandanus sp.; E, young antipodal cells of Sparganium simplex; F, cell formation in embryo sac of Sparganium; G, diagram of the typical angiospermous embryo sac; sy, synengids; o, egg; pn, polar nuclei; ant, antipodals; H, embryo sac of Anthurium violaceum; ant, antipodal cells.

generally have definite cell walls. The two free nuclei are the polar nuclei and as a rule fuse into a single endosperm nucleus. The antipodal cells are generally recognized as representing the sterile prothallial tissue, and typically are three in number. Sometimes the antipodal cells may degenerate, but they may become greatly enlarged or may undergo repeated division so that they form an evidently active prothallial tissue which is concerned with the further development of the embryo sac and the embryo. This increased activity of the antipodal tissue is especially marked in some of the more primitive genera, particularly among the monocotyledons, e.g., Pandanus, Sparganium, and some of the Araceae. Conspicuous antipodal cells are also found in some of the dicotyledons, e.g., Ranunculaceae and some Compositae.

There are some marked exceptions to the typical 8-nucleate embryo sac. Sixteen nuclei are found in species of *Peperomia, Gunnera, Euphorbia*, and *Penaea*. In *Pandanus* the number is much greater, sometimes as many as 64 antipodal nuclei being found.

Peperomia is a notable exception to the typical development of the embryo sac. This develops from the inner of two cells formed by the division of the archesporial cell. The first division of the embryo sac nucleus is a reduction division, and the four nuclei resulting from the next division are arranged tetrahedrally, recalling a typical spore-tetrad division. Each of the four nuclei undergoes two divisions, so that there are 16 in the embryo sac instead of the usual 8. Also there is no bipolar arrangement of the nuclei. The egg apparatus has only one synergid. The other 14 nuclei may all fuse into one very large endosperm nucleus, but several of them may become cut off by walls forming small cells attached to the wall of the embryo sac.

A somewhat similar condition is found in some species of *Euphorbia*, where four groups of four nuclei occupy the apex, base, and sides of the embryo sac. There are a typical egg apparatus and four free nuclei which do not seem to fuse into an endosperm nucleus.

A condition somewhat like that in *Peperomia* is found in *Gunnera*, where there are also 16 nuclei. Previous to the final division two nuclei are found at the micropylar region and six at the antipodal end. With the final division there are 4 micropylar and 12 antipodal nuclei. Six of the latter develop cell walls and form a group of conspicuous antipodal cells. There is a typical egg apparatus and the fourth nucleus functions as a polar nucleus which fuses with the 6 free antipodal nuclei to form a lower endosperm nucleus, much as in *Peperomia*.

In *Pandanus* the first stages follow the usual course and there are 2 micropylar and 2 antipodal nuclei. The 2 micropylar nuclei divide once and there is the formation of a typical egg apparatus and a polar nucleus.

The antipodal nuclei divide repeatedly, forming usually 12 large free nuclei. By further division there may be formed more than 60 nuclei, which in the later divisions are separated by cell walls and form a mass of prothallial tissue. Some of the nuclei become free and assume the role of polar nuclei, fusing with the upper polar nucleus into a large endosperm nucleus.

While the increase in the number of antipodal cells in forms like Gunnera and Pandanus is probably a primitive condition, associated with the increased number of nuclei before fertilization takes place, there are other instances where the embryo sac has the typical structure with three antipodals, which (usually after fertilization) may show active growth and undergo repeated division into a large number of cells. This is very marked in Sparganium. The Ranunculaceae often have very conspicuous antipodals, which doubtless play an important role in the further development of the embryo sac. Sometimes the cells divide, but more commonly the division is restricted to the nuclei, many forms having very large multinucleate antipodals.

The occurrence of highly developed antipodals in so many families generally regarded as relatively primitive makes it probable that this is really a primitive condition, i.e., the primary prothallium is better developed, as one would expect in the lower types of angiosperms.

A puzzling case is the frequent occurrence of highly developed antipodal structures in many Compositae—generally regarded as the most highly specialized of the angiosperms. Coulter explains this as indicating not a primitive condition but a highly specialized adaptation. "The antipodals of many of the Compositae are organized into an aggressive haustorium which can only be regarded as a very specialized organ." Coulter has described many other examples of the haustorial function of the antipodals.

POLLINATION AND FERTILIZATION

The transfer of the pollen spores to the receptive stigma of the flower is effected in various ways. Many primitive flowers, like those of the oaks, the poplars, the grasses, the date palm, etc., are "anemophilous," depending on wind for the transport of the pollen. This necessitates the development of a very large amount of pollen. A great economy in the amount of pollen is accomplished in the very great number of "entomophilous" flowers, where cross-pollination is secured through insect aid. Occasionally other animals have the same role—notably such birds as the American humming-birds and the "sun birds" of South Africa and Asia. The mutual adaptations between flowers and insects have doubtless played a most important role in the evolution of both angiosperms and insects.

¹ Coulter and Chamberlain, Angiosperms, p. 103.

The pollen spore falling on the stigma promptly emits the pollen tube, which penetrates the conducting tissue of the style very much as a fungushypha would do and perhaps, in a sense, might be regarded as a parasitic organism. Reaching the ovary cavity it may at once enter the micropyle of an ovule, or it may grow for a time along the ovary wall or the funiculus of an ovule before it enters the micropyle and, penetrating the overlying nucellar tissue, enters the apex of the embryo sac, where it either pushes between the synergids or sometimes destroys one of them, before reaching the egg into which one of the two male nuclei is discharged and fuses with the egg nucleus. The second male nucleus is discharged into the cavity of the embryo sac and, in many cases at least, unites with the endosperm nucleus.

THE ENDOSPERM

It has been suggested that the fusion of the second male nucleus with the endosperm nucleus is equivalent to a fertilization or sexual process; but it is not easy to accept this interpretation in connection with the multiple fusion of the polar nuclei in such cases as Gunnera, Peperomia, and Pandanus, where there is an increase to 16 or more nuclei in the embryo sac before fertilization. Just what is the significance of this compound nuclear-fusion is not clear-whether the endosperm is to be regarded as the equivalent of the prothallial tissue of the gymnosperm or as a special nutritive tissue peculiar to the angiosperms it is difficult to determine. From a study of the development of the embryo sac in Pandanus, where the antipodal tissue before fertilization is exactly like that of the subsequently developed endosperm, it might be inferred that both endosperm and antipodals are prothallial structures. This conclusion was expressed by Coulter after a careful examination of the various theories that have been proposed concerning the nature of the endosperm. Exceptionally the formation of endosperm may develop without the fusion of the polar nuclei, and in some cases, e.g., Naias, may be almost entirely absent. The endosperm in the angiosperms resembles so closely that of the gymnosperms that it is simpler to assume that the nuclear fusions in the embryo sac act merely as a stimulus to the growth of the endosperm rather than to picture the endosperm as an embryo which has assumed the purely vegetative function of nourishing the embryo formed from the egg cell.

The fusion of the polar nuclei may occur before or after the fertilization of the egg cell. From the division of the fusion-nucleus, in the typical embryo sac, a large number of free nuclei are formed which are embedded in a parietal layer of cytoplasm, resembling the corresponding stage in most gymnosperms. The formation of cell walls between the free nuclei results in a parietal layer of cells, whose growth and division are centripetal; and finally the embryo sac is filled with cellular tissue.

There are many variants from the usual endosperm formation. The first division of the primary endosperm nucleus may be followed by a division wall and no free cell formation may occur—e.g., Peperomia, Sarcodes, some Araceae. Schaffner states that in Sagittaria variabilis a cell wall divides the embryo sac into an upper portion, which develops a typical cellular endosperm, and a lower chamber which remains undivided, although there is limited division of the nucleus. A somewhat similar condition occurs in Nymphaea, in Saururus, and in certain Araceae, e.g., Anthurium violaceae.

While the endosperm is primarily concerned with the storage of reserve food materials for the growth of the embryo and the early stages of germination, the storage function may be taken over by the embryo itself in the "exalbuminous" seeds, where the embryo finally completely fills the seed cavity. Familiar examples are the legumes and the seeds of the various fruits like the apple, plum, etc.

In a number of the lower dicotyledons, e.g., Piperales and Centrospermae, the development of the endosperm is restricted and the reserve food is mainly stored in the surrounding tissue of the nucellus. This nucellar tissue is known as "perisperm." The endosperm, which immediately surrounds the embryo, probably serves as an intermediary between the perisperm and the small embryo. Perisperm is also found in some monocotyledons, e.g., Canna; and in some of the Araceae the embryo sac is relatively small and the basal (chalazal) region of the ovule is much enlarged and may perhaps be compared with the perisperm of the Piperales.

THE SEED

The integument (testa) of the seed may be thin and membranaceous, as in the kernel of various stone fruits, like the cherry or peach, where the seed is protected by the hard pericarp. Usually the testa is a firm shell which protects the embryo and the surrounding endosperm. Sometimes there are appendages of the testa, like the hairs in cotton or the wings in Catalpa, which facilitate the distribution of the seeds by wind.

THE FRUIT

In the angiosperms the stimulus due to pollination extends beyond the transformation of the ovule into a seed. Sometimes at the time of pollination the ovule is still rudimentary and it develops during the slow growth of the pollen tube through the tissues of the pistil. In all cases the carpels are stimulated into growth and keep pace with the growth of the seeds within the ovary. The resulting structure is the "fruit." In the angiosperms the fruit varies greatly. It may be a dry pod; an indehiscent "caryopsis," like the grains of the cereals; a fleshy fruit, like the berry of

a currant; or a "drupe," characteristic of the stone fruits. Besides these true fruits are such pseudo-fruits as the strawberry and fig. In these the very simple seed-like fruits are embedded in edible pulp, which is developed from the fleshy receptacle at the apex of the floral axis. In the fig the many small flowers and later the minute, one-seeded fruits are borne in the hollow receptacle formed from the enlarged fleshy stem.

The fruit includes the seeds and the pericarp or wall formed from the carpels. The simplest form is the follicle—a dry capsule formed from a single carpel. More commonly the fruit is syncarpous and may be a dry capsule, which commonly opens by longitudinal fissures which follow the line of separation between the carpels (septicidal dehiscence), or each carpel is split longitudinally (loculicidal dehiscence). The follicles of many Ranunculaceae—e.g., Caltha, Helleborus, and the legumes (bean, pea)—are apocarpous capsules.

In a good many forms the pericarp adheres closely to the seed and forms an "indehiscent" fruit. Such indehiscent fruits are the "nuts" of hazel, acorns, the "caryopsis" or "grain" of the grasses, and the seed-like

fruits (achenes) of the Compositae.

Where the pericarp is fleshy, the fruit may be: a "berry" in which the endocarp and mesocarp are pulpy; or a drupe, or stone fruit, where the endocarp is composed of very hard tissue—the "stone"—enclosing the seed. Among the monocotyledons many palms, like the date and coconut, are examples of stone fruits.

THE EMBYRO IN MONOCOTYLEDONS

The embryo in the angiosperms, in the ripe seed, varies greatly in structure. It may be reduced to a few cells and show no trace of differentiation; or it may have the primary organs of the sporophyte, leaves, axis, and root, as well as the primary tissue complete before the seed germinates. In such cases, e.g., Leguminosae and Compositae, the embryo sporophyte entirely fills the seed cavity, the endosperm having completely disappeared. Such seeds are known as exalbuminous. In these seeds the reserve food is stored mainly in the massive primary leaves—the cotyledons. Between these extremes are all degrees of differentiation of the embryo.

Very commonly a definite suspensor is formed, thus recalling the embryo in the Coniferales but with a fundamental difference. In the typical gymnosperms there is the formation of free nuclei in the zygote, followed by free-cell formation much like that in the endosperm. In the angiosperms the first division in the zygote is by a cell wall, as are all subsequent divi-

sions in the embryo.

The first division in the zygote usually follows closely on fertilization

and the development of the embryo proceeds with that of the endosperm.

Sometimes, however, the zygote remains undivided for a long time and the embryo remains small and quite undifferentiated up to the time the seed is ripe. Thus in *Peperomia* the embryo in the ripe seed is a small globular mass of about 15 similar cells and in the orchids a similar condition prevails.

Usually, however, the embryo in the ripe seed shows a certain amount of differentiation, although it may be very small. The first division wall is transverse, and frequently the basal cell does not divide but may become greatly enlarged, forming a sort of haustorium. This is especially marked in some simple aquatic monocotyledons, e.g., Sagittaria, Alisma, and Naias.

The next division is transverse and the embryo forms a row of three cells. This three-celled filament Coulter calls a "proembryo," the embryo proper being developed mainly from the terminal cell. The intermediate cell is next divided transversely, forming a short secondary suspensor. Naias flexilis may be taken as an example of this type of embryo in the monocotyledons.

In some of the Araceae, e.g., Aglaonema, after the primary transverse division of the zygote the basal cell does not become enlarged but may divide once or twice. No functional suspensor is formed. This is true of other Araceae examined, e.g., Lysichiton. The absence of a suspensor

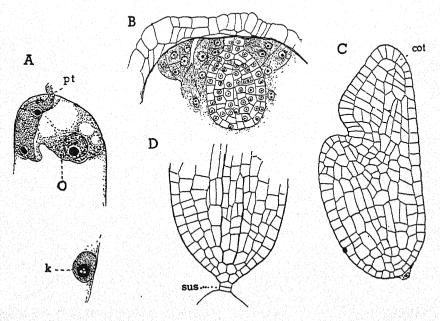


Fig. 297.—A, embryo sac (Naias?) showing entrance of pollen tube, pt; k, endosperm nucleus; B, embryo of Sparganium simplex, surrounded by endosperm; C, embryo of Naias flexilis; D, older embryo of Naias, basal region; sus, suspensor.

seems to be correlated with the complete inclusion of the embryo by cellular endosperm. Contrasted with this condition is the extraordinary development of the suspensor as a multicellular haustorium. This is especially notable in some Leguminosae, e.g., Lathyrus and Laburnum.

The young embryo of *Naias* consists of the enlarged primary suspensor cell, a secondary suspensor of two cells, and the terminal cell. In the terminal cell there is formed a transverse wall followed by a median vertical wall in each cell. The embryo now consists of the enlarged basal cell, two short secondary suspensor cells, and a globular body, composed of forcells arranged like the quadrants of a sphere. Each of the quadrants next divides by an octant wall. From the upper octants the single cotyledon develops, from the lower the stem and root.

The differentiation of the primary tissue systems is initiated at an early stage of development. The formation of the primary tissues is very evident in the central region from which the stem apex and root are formed. In the cotyledon they are not so clearly defined. A cross section of a median section of the young embryo shows a group of four cells, the plerome, separated from the dermatogen by a single layer of periblem cells. At a later stage there is an axial vascular bundle which extends from the cotyledon into the root, a condition very much like that in the embryo-sporophytes of the eusporangiate ferns and *Isoetes*.

The cotyledon includes the whole terminal portion of the embryo. There is a marked enlargement of the middle region, corresponding to the stem segment. This growth is mostly on one side of the stem, and there is formed a depression at the base of the cotyledon, marking the apex of the stem. The later growth of the cotyledon is mostly at the base, and there is formed a stipular sheath which finally completely envelops the stem apex. With the growth of the stem apex a vascular strand is formed joining the primary axial bundle of the cotyledon and root. This bundle is probably not strictly cauline but is associated with the second leaf.

A peculiarity of the primary root in Naias is the absence of a root cap. The dermatogen extends over its apex, but no definite root cap can be demonstrated. It thus differs from other monocotyledons that have been examined. The embryos of other simple aquatic monocotyledons are much like that of Naias but show some points of difference. Thus Zannichellia has a well-developed root cap, and both stem apex and cotyledon are formed from the terminal segment of the proembryo. This terminal origin of the stem is not common in monocotyledons but is typical of the dicotyledonous embryo. Lilaea in its first stages resembles Naias, but its root is of lateral origin, as it is in Isoetes, suggesting the possibility that the basal segments of the embryo, including the suspensor, might be interpreted as equivalent to the foot of the fern embryo.

Sparganium represents a somewhat different type. In S. ramosum Hegelmaier describes a three-celled proembryo but with no enlargement of the basal cell. S. simplex agrees closely with S. ramosum in the further development of the embryo. Of the three primary cells of the proembryo the stem apex, the cotyledon, and part of the root all are developed from the terminal cell of the proembryo. As in the Araceae the embryo is completely surrounded by cellular endosperm and develops no functional suspensor.

Where endosperm is present in the ripe seed the cotyledon acts as haustorium, and sometimes, as in the grasses and palms, develops a special organ, the scutellum, which remains within the seed, only the basal part of the cotyledon emerging as a sheath, within which the apical bud ("plumule") is contained. Where no endosperm is present, the cotyledon develops at once into the first foliage leaf.

Where both stem apex and cotyledon are formed from the terminal cell of the proembryo, as in Zannichellia—a condition also noted for some other monocotyledons, e.g., Dioscoreaceae and Commelynaceae—the relation of stem apex to cotyledon is in a way intermediate between that of the typical monocotyledons and that of the dicotyledons. The monocotyledonous Agapanthus, according to Coulter, may sometimes have two cotyledons.

THE EMBRYO IN DICOTYLEDONS

The enormous number and variety of the dicotyledons is reflected to some extent in the character of the embryo; but little relatively has been done in a critical study of the earliest stages, and it is impossible to select a truly typical example. The often illustrated Capsella may be taken for comparison with the monocotyledonous type illustrated by Naias.

As in the latter there is a proembryo consisting of a large basal cell and several suspensor cells. The terminal cell, as in Naias, increases in size and becomes divided into equal octant cells, exactly as in Naias. The first transverse walls separate the embryo into a cotyledonary and hypocotyledonary region. The upper suspensor cell undergoes further growth and division, and from it the root apex and root cap are developed. The primary tissues—dermatogen, periblem and plerome—are formed in the same way as in Naias.

The globular form of the young embryo is soon lost, and in longitudinal section it appears heart-shaped, indicating the beginning of the two equal cotyledons. Between these the stem apex is differentiated. The young embryos of a very large number of dicotyledons are of the same type as Capsella, but there is much difference in the development of the suspensor.

As in the monocotyledons there are many departures from the predomi-

nant type. The *Peperomia* type has already been referred to—an undifferentiated cell mass with no suspensor. In *Nelumbo*, Lyon states that the large undifferentiated spherical embryo has no suspensor and recalls that of some of the monocotyledonous Araceae. A similar condition was found by Conard in *Nymphaea*.

Among the most marked departure from the type occurs in some of the Leguminosae. Guignard found in some of these, e.g., Lathyrus, Lupinus, and Laburnum that the suspensor cells increase greatly in size and number, sometimes becoming multinucleate. The proembryo is sometimes (Laburnum) a large globular mass of cells. These greatly developed suspensor or proembryonic structures are doubtless haustoria, providing nourishment to the developing embryo.

The condition of the embryo in the ripe seed shows much the same variation as in the monocotyledons. In certain families, e.g., Ranunculaceae and Papaveraceae, the embryo is very small and undifferentiated and is embedded in abundant endosperm. Contrasted with these "albuminous" seeds, are the "exalbuminous" seeds of the Leguminosae and most Rosaceae and Pomaceae. In these the cotyledons are greatly thickened and contain most of the stored food materials in the seed. The cotyledons may differ but little from the ordinary leaves but they are generally of different form from the later leaves. In the exalbuminous forms the cotyledons may remain permanently within the seed coats or they may be finally withdrawn and develop chlorophyll, functioning as foliage leaves.

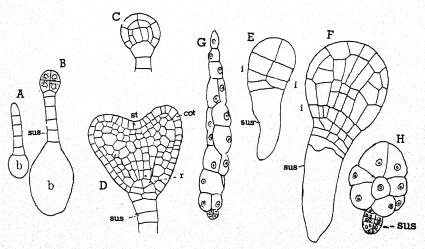


Fig. 298.—Embryos of dicotyledons. A-D, capsella; b, basal cell of suspensor; st, stem apex; cot, cotyledons; E, F, embryos of Senecio aureus; G, Cicer arietinum; H, Anthyllis tetraphylla, with very large multicellular suspensors (E, F, after Mottier; G, H, after Schnarf).

POLYEMBRYONY

As in many gymnosperms there are many cases where more than one embryo may be found in the seed. A familiar case is that of orange seeds which sometimes sprout within the fruit. The origin of the extra embryos, in such cases, may differ. Strasburger found in Funkia ovata, the orange, and some other forms, that the embryos develop as vegetative outgrowths of the nucellar tissue and grow into the cavity of the embryo sac. In Funkia, although the egg is fertilized, it does not develop a normal embryo. In the Liliaceae, secondary embryos may be formed from the suspensor of the primary embryo. Jeffrey cites Erythronium Americanum, and Ernst found a similar condition in the tulip. In these cases only one embryo matures.

The development of "apogamous" embryos from cells of the embryo sac—e.g., synergids, antipodal cells, or cells of the endosperms—have been noted in many cases. Somewhat different is the occurrence of parthenogenesis where the unfertilized egg may develop an embryo. This has been found in species of *Antennaria*, *Alchemilla*, and *Thalictrum*.

CHAPTER XXIV

ANGIOSPERMS—MONOCOTYLEDONS

Notwithstanding the unmistakable relationships existing among the angiosperms, it is becoming more and more evident that their arbitrary division into two co-ordinate subclasses, monocotyledons and dicotyledons, is not entirely natural. That there have been more than two main lines of evolution from some older stock that no longer exists seems certain; and it is much more likely that instead of two primary divisions or subclasses we should recognize a much greater number—subclasses or phyla based upon something more than the superficial characters which often are deemed sufficient.

A critical examination of the differences commonly accepted as distinguishing the two subclasses will show that none of them are really adequate. We may cite "typical" flowers, like the lily or the geranium, as illustrating the floral characters of the two subclasses: but if, instead, we should select the flowers of *Sparganium* and *Populus*, how are we to say which is monocotyledonous, which dicotyledonous? The explanations that these simple flowers are "reduced" from the type forms is not very convincing, especially as it happens that these are among the oldest known angiosperms.

The herbaceous stem with scattered "closed bundles" characteristic of most monocotyledons and practically duplicated in such dicotyledons as Peperomia and Podophyllum and likewise the broad net-veined leaves found in so many dicotyledons occur in Trillium, Smilax, and many Araceae. Even the embryos are not always "typical": Abronia, Cyclamen, and Ranunculus Ficaria are "pseudo-monocotyledonous," and the embryos of Zannichellia and Dioscorea have a terminal stem apex and a lateral cotyledon like that in dicotyledons. In short, it is clear that no satisfactory criteria can be established which indicate such fundamental differences as are implied in the recognition of monocotyledons and dicotyledons as primary divisions of the angiosperms.

Naturally there has been much speculation as to the relationships existing between the two groups. The prevalent view is that the monocotyledons have originated from ancestors related to the living Ranales and hence must be regarded as more recent than the dicotyledons. Strasburger concluded that from the Gnetales three independent lines of dicotyledons developed and from one of these the monocotyledons later branched off. It is prob-

able that Strasburger's conclusions have strongly influenced the later theories of the derivative character of the monocotyledons. Somewhat later Kny decided that the monocotyledons were derived independently from the Filicineae; and, still later, Solms-Laubach came to the conclusion that the two divisions of the angiosperms arose independently from gymnosperms.

The more recent theories of Hutchinson and others that the angiosperms are derived from a common ancestor related to the Bennettitales has already been referred to. This theory assumes that the dicotyledonous orders Magnoliales and Ranales are the most primitive and that from the latter the monocotyledons have been derived. Wettstein, like Strasburger considers the dicotyledons as polyphyletic but also regards the Ranales as the ancestors of the monocotyledons. Engler, as already noted, finds satisfactory neither the theory of the origin of the angiosperms from Bennettitales nor that from Gnetales, and predicates the hypothetical ancestral stock, protangiosperms, from which arose numerous independent phyla of both monocotyledons and dicotyledons, neither giving rise to the other. However, if one is derivative, he thinks the dicotyledons the older. Of the living families, he concludes that the Piperales and the Pandanales most nearly resemble the hypothetical protangiosperms. The absence of fossil protangiosperms Engler explains by assuming that many of them were herbaceous and not likely to leave recognizable fossils, while the tissues of woody species would not be readily distinguishable from those of true angiosperms.

The possibility of a direct derivation from fern-like ancestors is also considered by Engler, who recalls the similarities in the vascular bundles of some of the eusporangiate ferns, especially the Ophioglossaceae and the angiosperms. Kny calls attention to the fact that it is the monocotyledons whose embryos most nearly resemble those of the ferns. The marked resemblance in the embryo, as well as the structure of the older sporophyte, of *Isoetes* to that of some of the monocotyledons has been cited by Coulter as perhaps indicating a real relationship.

MONOCOTYLEDONS

The monocotyledons are much less numerous than the dicotyledons, and are on the whole less specialized. There is also greater uniformity in both the tissues and the floral structure. In size they range from the almost microscopic Wolffia, a floating aquatic, consisting of an oval mass of tissue with no definite external organs, to giant palms with massive trunks 30–40 meters in height, and leaves in some cases 10–15 meters in length—the largest found in any plants. Among the palms are the climbing rattans, Calamus, spp., some of which reach a length of several hundred feet—the longest plants known.

Many families of monocotyledons are cosmopolitan. Such families as

the grasses and sedges are important constituents of the vegetation of most parts of the world. A majority of the aquatic angiosperms are also monocotyledons, and these play the most important role in swamp and marsh vegetation. Such are the strictly aquatic pondweeds—e.g., Naias, Zannichellia, and Potamogeton—and many marsh plants, like the reeds, sedges, and rushes. A considerable number are found in the sea, like the eelgrass (Zostera), Phyllospadix, Cymodocea, Posidonia, and others living in salt water.

Of the terrestrial forms, the grasses are the most widespread and abundant, and almost the only monocotyledons in temperate climates to dominate the vegetation of large areas, like the prairies of the central United States. In the warmer parts of the world palms and other arboreal types, like some species of Yucca, Dracaena, and Aloe, often are a conspicuous feature of the vegetation. Parasites and saprophytes are unusual, although among the Orchidales there are a number of genera in which no chlorophyll is present.

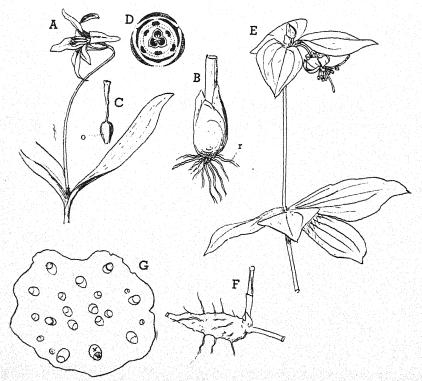


Fig. 299.—A, flower and leaves of Erythronium americanum; B, bulb and roots of the same; C, pistil; D, floral diagram; E, Medeola virginiana; F, rhizome of Medeola; G, section of stem of Erythronium.

ANATOMY

The stem.—The stem in most monocotyledons is limited in growth, and there is often a subterranean stem—rhizome, bulb, or tuber—from which aerial shoots are produced. After the shoot has developed flowers and fruit, it dies. There are, however, a good many forms, mostly in the tropical and subtropical regions, where there is a permanent stem. The palms are the most important, but the screw pines—(Pandanus), Aloe, Dracaena, Yucca, etc.—and in the wet tropics some Araceae, e.g., Monstera and Philodendron, show the same character. In the palms branching is usually absent; but there are some exceptions, e.g., the "Dom. palm," Hyphaene,

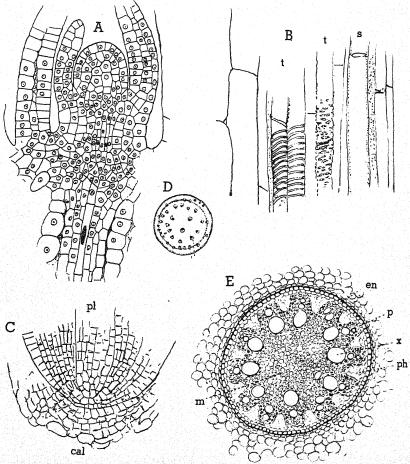


Fig. 300.—A, stem apex of Naias flexilis; B, vascular bundle of stem of Iris florentina; t, tracheary tissue; s, sieve tubes; C, root apex of Zannichellia palustris; D, cross section of stem of Iris xiphium; E, section of primary root of Phoenix canariensis.

where there is a regular dichotomous branching. *Pandanus* and a good many Liliaceae, e.g., *Dracaena*, *Yucca*, and *Cordyline*, are arborescent species, and are freely branched, and exhibit a secondary increase in the diameter of the stem.

A cross section of the stem in most monocotyledons shows a parenchymatous ground tissue with many isolated "closed" collateral or "amphivasal" vascular bundles; i.e., no cambium is present. Where the stem shows secondary thickening, e.g., in *Dracaena*, *Aloe*, *Yucca*, etc., there is present in the cortex a zone of meristematic tissue, in which are formed on its inner side new vascular bundles surrounded by new ground tissue. Concentric growth rings comparable to those in gymnosperms and dicotyledons are not usually recognizable. The outer portion of the meristematic zone develops only parenchyma.

A recent study of this secondary growth has been made by V. I. Cheadle, who investigated a number of American types, e.g., Yucca, Dasylirion, Nolina, as well as Dracaena, Aloe, and other Old World genera. Cheadle states that the bundles may be either collateral or amphivasal—i.e., with the phloem entirely surrounded by the xylem—but the two types are constant within a genus; e.g., in Yucca the secondary bundles are always collateral, in Dracaena always amphivasal.

The stem bundles in the monocotyledons are all leaf traces. They may be surrounded by a sheath of fibrous cells which act as mechanical or strengthening tissue, since the xylem is composed entirely of thin-walled vessels which serve only for water conduction. Other mechanical elements are fibers and collenchyma in the hypodermal region.

The leaf.—The simple, often elongated, narrow leaf, with parallel veins, is characteristic of the majority of monocotyledons; but there are numerous exceptions. Thus in Trillium, Smilax, and many Araceae—e.g., Pothos, Anthurium, Symplocarpus, Lysichiton—the broad leaves have reticulate venation and closely resemble the typical dicotyledonous leaf. Among the Araceae certain genera like Arisaema and Syngonium have true compound leaves, a condition rare in monocotyledons.

Among the monocotyledons are many species having leaves of gigantic size. The leaves of some palms, like Caryota, Attalea, and Raphia, which may be ten to fifteen meters in length, and those of some of the bananas (Musaceae) are quite unmatched by the leaves of any dicotyledons. The nearest approach to these megaphyllous forms is to be found among the cycads and such ferns as the Cyatheaceae and Marattiaceae. One might be tempted to suggest that this might indicate some very remote relationship between monocotyledons and ferns, as both show a marked subordination of the axis to the leaves.

The leaf base is very often expanded like that of Isoetes and many

ferns, and may become a conspicuous sheath surrounding the internodes of the stem. This is very characteristic of the grasses and sedges and of many submersed aquatic genera, e.g., *Potamogeton*. In many palms also, like the royal palm (*Oreodoxa*) and *Areca*, the leaf sheath is very conspicuous.

It has sometimes been suggested that the leaf of the monocotyledons is not really homologous with that of the dicotyledons but only with the base and petiole—somewhat analogous to the "phyllode" of certain acacias. This view has been supported by Mrs. Agnes Arber. The lamina of the leaf is explained as a "pseudo-lamina" not homologous with the leaf lamina in the dicotyledons. This theory, however, is difficult to apply to such leaves as those of the Araceae, the Alismaceae, and other forms where the leaf has a petiole and lamina directly comparable to those of a typical dicotyledonous leaf, and certainly might much more plausibly be considered to be really homologous. It would be difficult to believe that the leaves of Saururus and Dioscorea, respectively dicotyledon and monocotyledon, for example, are not truly homologous structures—i.e., that one has a "true" lamina, the other a "pseudo-lamina."

The leaf base may persist as an enveloping scale in some bulbs, e.g.,

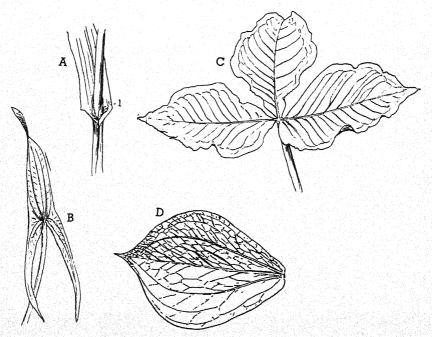


Fig. 301.—A, Dactylis glomerata, showing leaf sheath and ligule, l; B, leaf of Sagittaria variabilis; C, leaf of Arisaema triphyllum; D, leaf of Trillium grandiflorum.

onion and tulip; and the stem leaves may be reduced to small scales in species having no chlorophyll, like the saprophytic coralroot (Corallorhiza). In the so-called "smilax" (Asparagus medeoloides), the leaves are minute scales, subtending leaf-like shoots, phylloclades, which replace the leaves. Reduced leaves or bracts are common in connection with inflorescences, and sometimes these become conspicuously colored, and probably perform the function of the showy petals in the typical flower. In the Araceae the large white spathe of the common calla lily and the scarlet spathe of some species of Anthurium are familiar examples of this. Others are the large, brilliantly colored bracts of the Bromeliaceae, and some species of bananas (Musa) and the related Heliconia.

Roots.—The primary root of the monocotyledonous embryo never persists as a taproot but is soon replaced by secondary roots. The roots in some of the arborescent types like the palms and screw pines (Pandanus) may reach considerable thickness. Aerial roots are found in many epiphytic orchids and Araceae; and in the screw pines and some palms stout aerial roots may arise from the base of the trunk and penetrate the ground, forming an extensive root system which supports the trunk.

The structure of the roots is similar to that of the pteridophytes, i.e., is "radial" with alternate plates of xylem and phloem. In most cases there is no secondary growth in thickness; but in such cases as *Dracaena*, where

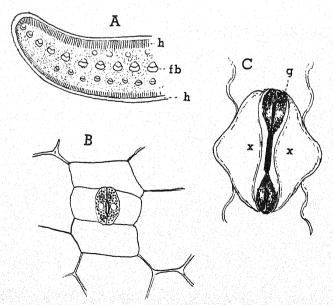


Fig. 302.—A, section of leaf of Agave americana; h, hypoderma; jb, vascular bundles; B, stoma of Tradescantia zebrina; C, stoma of Zea Mays; g, guard cells; x, accessory cells.

there is regular secondary growth in the stem, the roots have been shown to have some secondary thickening. Whether or not the massive roots of *Pandanus* show such secondary thickening has not apparently been investigated.

THE FLOWER

Among the monocotyledons are some genera in which the flower is reduced to its simplest form, i.e., a single carpel or stamen. In Naias both carpel and stamen are formed from the apex of the floral axis and are extraordinarily similar in structure. The anther and the ovule are both provided with an integument, and are enclosed in an envelope, which in the case of the ovule is generally interpreted as a carpel. Nearly as simple are the flowers of certain Araceae, e.g., Aglaonema, Spathicarpa. In these, however, the flowers are aggregated into an inflorescence, and this is true also of some of the other primitive families, e.g., Pandanaceae and Typhaceae. In the former the flowers are dioecious; the Typhaceae and Araceae, with very few exceptions, are monoecious. The individual flowers are either quite destitute of a perianth, or this is reduced to inconspicuous scales.

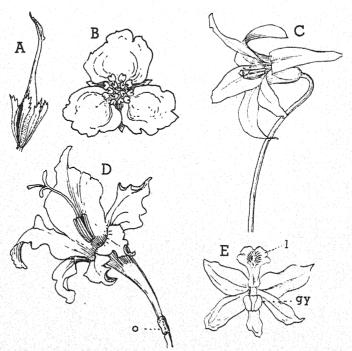


Fig. 303.—A, pistillate flower of Sparganium simplex; B, staminate flower of Sagittaria variabilis; C, hypogynous, actinomorphic flower of Erythronium; D, epigynous zygomorphic flower of Gladiolus; o, ovary; E, an orchid, Calopogon; l, labellum; gy, gynostemium.

A somewhat more advanced condition is represented by the Alismaceae. A familiar example is the "arrowhead," Sagittaria, the showy white flowers of which have a perianth of three sepals and three conspicuous white petals; some of the flowers have a central group of stamens, the others a similar group of free carpels. These apocarpous flowers are much like those of some of the lower dicotyledons and are sometimes believed to be related to them.

In most of the monocotyledons the flowers are bisporangiate ("hermaphrodite"), and the perianth is composed of two cycles of three members, usually much alike in appearance and petaloid in texture. These may be free like those of most of the Liliaceae—e.g., Lilium, Tulipa, Calochortus—but not infrequently the perianth segments are united into a tube. The hyacinth and the lily of the valley are familiar examples. The stamens in the Liliaceae are in two sets of three, like the perianth. It is generally stated that there are only three carpels; but Miss Sanders in her study of carpel structure recognizes six in the Liliaceae. The united carpels form a three-celled ovary. The ovary is completely free from the perianth and the stamens, and is thus "hypogynous," "superior." In the nearly related Amaryllidaceae, e.g., Narcissus, Amaryllis, and Crinum, the perianth segments are united into a tube the base of which is coherent with the "inferior" ovary of the "epigynous" flower.

The Iridaceae, e.g., Iris, Gladiolus, and Ixia, differ from the Amarylli-daceae in having the stamens reduced to a single cycle of three. In some genera, e.g., Ixia and Sisyrinchium, there are six similar perianth segments, and the flower is radially symmetrical, "actinomorphic." Iris, with a similar arrangement of the perianth, has two perianth cycles different in form. In Gladiolus the flower is bilaterally symmetrical or "zygomorphic." The specialized characters in the Iridaceae are probably adaptations to insect

pollination, and they are typically entomophilous.

The most highly specialized monocotyledonous flowers belong to the Scitaminales, especially the ginger and Canna families, and to the Orchidales. The flowers in these orders are always epigynous, and are usually characterized by marked zygomorphy. In the gingers and Cannas, only a single stamen is functional, the others being changed into petal-like "staminodia," which constitute the showy part of the flower. The true petals are relatively inconspicuous. In most of the orchids only a single fertile stamen is produced; the others are absent or are represented by inconspicuous staminodia. The single fertile stamen is united with the upper part of the pistil into a characteristic organ, the "gynostemium" or "column." The flowers in the monocotyledons may be borne singly on a slender "scape" like the tulip or the daffodil, or there may be an inflorescence having many flowers. The inflorescence may reach enormous

size, like that of the century plant (Agave) and those of some species of Yucca and of many palms.

The fruit may be: a dry capsule, as in Lilium; an achene, as in Sagutaria; a "caryopsis," as in most grasses; a pulpy berry, as in Asparagus and Convallaria; or a stone fruit, as in many palms. In the pineapple and some other bromeliads, the "fruit" is formed from the fusion with the floral axis of the flowers of the crowded inflorescence, whose perianths, together with the enlarged floral axis, develop a juicy pulp, the whole forming the familiar pineapple.

CLASSIFICATION

As might be expected, there have been many attempts to group the numerous families into orders. The arrangement most commonly adopted at present is that of Engler (Syllabus der Pflanzenfamilien). Engler recognized ten orders, to which later was added another, Triuridales. Coulter (Morphology of Angiosperms) accepts Engler's orders but makes some changes in terminology more in accordance with recent usage. Thus Engler's "Spathiflorae" is replaced by "Arales," and "Principes" by "Palmales." We shall, therefore, recognize here eleven: viz., (1) Pandanales; (2) Helobiales; (3) Triuridales; (4) Glumales; (5) Palmales; (6) Synanthales; (7) Arales; (8) Farinales; (9) Liliales; (10) Scitaminales; (11) Orchidales. (Hutchinson, in a recent review of the monocotyledons, recognizes 28 orders under three divisions.)

The first seven orders are characterized by simple flowers, often diclinous, sometimes with numerous stamens. The perianth for the most part is inconspicuous or even completely absent. Among the Helobiales, however, are genera with conspicuous perianth—e.g., Sagittaria, Butomus, and Hydrocleis—which are much like the flowers of the Ranales among the dicotyledons.

The four latter orders include all the highly specialized floral types, like the lilies, *Iris*, and the orchids, and have often very showy flowers and special adaptations to cross-pollination by insects.

ORDER 1. PANDANALES

This order includes some of the simplest and presumably the most primitive of the monocotyledons. The pistillate flower may consist of a single carpel with no perianth. The stamens are indefinite in number. Three families are included by Engler in the Pandanales: Pandanaceae, Sparganiaceae, and Typhaceae.

The Pandanaceae include two genera, *Pandanus* and *Freycinetia*. They are all restricted to the Old World, but each genus is represented by a single species in Hawaii. The screw pines, *Pandanus*, are abundant in the Eastern

tropics but the species are not always clearly delimited. Some of them are trees of moderate size, others large shrubs. They are characteristic members of the strand floras, but there are also forest species.

They branch dichotomously, and the trunk is supported by numerous stout, stilt-like aerial roots, and sometimes such roots are developed from the branches. The long, narrow leaves with spiny margins are arranged

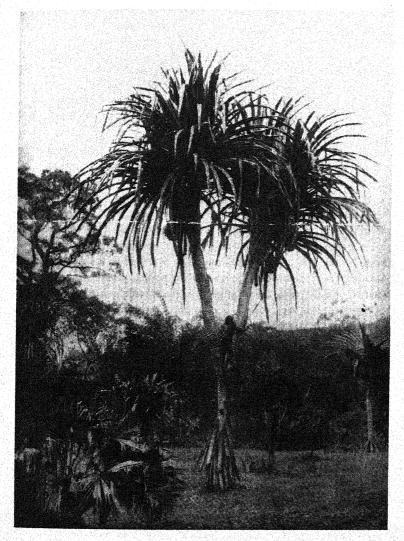


Fig. 304.—A screw pine, Pandanus sp., Peradeniya, Ceylon.

about the stem in a spiral series; hence the popular name. There is a secondary increase in thickness in the trunk like that in Yucca or Dracaena. Pandanus is dioecious. The pistillate flowers form a dense head, which in the smaller species is subtended by a single large bract and in the larger ones by several bracts surrounding the inflorescence.

The staminate inflorescence is composed of numerous branches upon which the flowers are borne. The ultimate divisions of the branches form sporangiophores, upon which are borne the very numerous stamens. It is not possible to determine the limits of a single flower.

The pistillate flower may consist of a single carpel, or there may be several carpels united. In *P. artocarpus* the single carpel is a slender, club-shaped body with the sessile stigma somewhat bent over. The single anatropous ovule is attached near the base to one side of the ovarian cavity. Where there are several united carpels in the flower the inflorescence forms a solid mass, and the mass of ripe fruits is often brightly colored and resembles a large pineapple.

The second genus, Freycinetia, differs a good deal in appearance from Pandanus. The species are mostly climbing plants, often reaching a great length, the slender stems bearing leaves much like those of Pandanus. The inflorescences are enclosed in conspicuous, white or red, fleshy bracts. The inflorescences are slender spikes, covered with crowded flowers. The staminate flower is a group of stamens with elongated filaments, surrounding an abortive ovary. The carpels are several, completely united into a compound pistil with very numerous ovules attached to the walls of the unilocular ovary. Surrounding the ovary are several abortive stamens. The ripe fruit is fleshy, with many minute seeds. While most species of Freycinetia are tropical, F. Banksii is common throughout most of New Zealand, extending beyond latitude 45 degrees south.

That the Pandanaceae are primitive forms is indicated by the female gametophyte. The embryo sac in *Pandanus* before fertilization contains over 60 nuclei—greatly exceeding that of any other known angiosperm.

The bur reeds (Sparganium) and the cattail (Typha) represent the two other families of the Pandanales. The two families, Sparganiaceae and Typhaceae, unlike the Pandanaceae, belong mainly to the temperate regions; but species of Typha are also tropical. Sparganium, except for a single species in New Zealand and Australia, is restricted to the North Temperate Zone.

Sparganium and Typha are aquatic, thus differing in habit from the Pandanaceae. They also are typically monoecious. The pistillate flowers occupy the basal and the staminate flowers the upper part of the inflorescence. In Sparganium the inflorescence is either a simple raceme or is branched. In Typha it is a cylindrical spike, the crowded pistillate flowers

developing minute one-seed fruits surrounded by numerous hairs. The stamens cover the upper part of the axis of the inflorescence, which extends above the pistillate region. The pistillate flower in Typha always consists of a single carpel, but in Sparganium it may be either a single carpel or two united carpels forming a bilocular ovary. In both Sparganium and Typha the staminate flower consists of several free stamens. In Sparganium the flower usually has a rudimentary perianth composed of six scales; in Typha there are numerous hair-like appendages but no definite perianth.

While the embryo sac of *Sparganium* has at the time of fertilization the typical 8-nucleate structure, there is later a remarkable development of the antipodal tissue comparable to that found in *Pandanus*; and in other

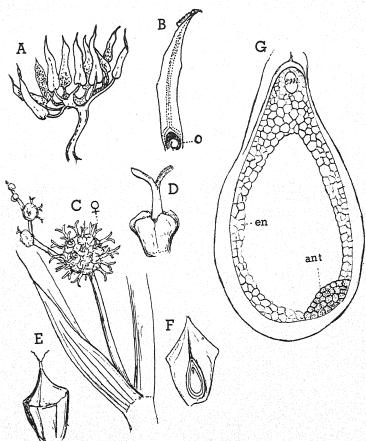


Fig. 305.—A, staminate flower of Pandanus Lais; B, pistillate flower of P. artocarpus; C, female inflorescence of Sparganium eurycarpum; D, single pistillate flower of the same; E, ripe fruit of the same; F, section of fruit; G, embryo sac of S. simplex, showing endosperm, embryo, and antipodals.

respects Sparganium is much more like Pandanus than is Typha. In all of the Pandanales the endosperm fills the seed and completely surrounds

the embryo.

On the whole, Sparganium is probably more nearly related to the Pandanaceae than to Typha, although the latter also shows more evidence of relationship with the Sparganiaceae than with any other family of the monocotyledons.

ORDER 2. HELOBIALES

The Helobiales include seven families with about 250 species, all aquatics, mostly of simple structure. Some of them, e.g., Naias, Zannichellia, and Potamogeton, are completely submersed and the leaves are delicate in texture, with no air spaces and no stomata. Others develop floating leaves, borne on long petioles, suggesting those of the water lilies, e.g., Hydrocleis and Elisma. Other genera, e.g., Sagittaria and Alisma, are amphibious, growing rooted in mud or shallow water and having upright, rigid leaf stalks and scapes bearing the flowers. The leaves in these genera have an

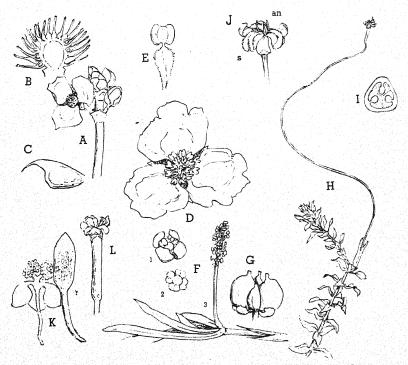


Fig. 306.—A, pistillate flower of Sagittaria variabilis; B, section showing the numerous carpels; C, ripe fruit; D, staminate flower; E, stamen; F, G, Potomogeton sp.; H, Elodea canadensis; I, section of ovary; J, flower; K, staminate flowers of Vallisneria; L, pistillate flower.

expanded lamina, showing a typical leaf structure, i.e., spongy mesophyll and numerous stomata. In floating leaves stomata are developed on the upper surface only. In the Alismaceae, e.g., Sagittaria and Alisma, the leaves show a reticulate venation like that of some dicotyledons, with which the Alismaceae have some other points in common.

The flowers in the Helobiales may consist of a single carpel or stamen, e.g., Naias and Lilaea, and the flower is destitute of any perianth. In Potamogeton there are four stamens, with petal-like appendages and four carpels but no perianth. In the Alismaceae there is a perianth with three sepals and three conspicuous petals. In Alisma there are six stamens and several free carpels; in Sagittaria, where stamens and carpels are borne in separate flowers, both stamens and carpels are more numerous than in Alisma. These more specialized types therefore show an approach to the definitely trimerous flowers of most of the higher monocotyledons; and some students of the latter, e.g., Lotsy, believe that the higher monocotyledons have all been derived from the Helobiales.

The most specialized family of the Helobiales is the Hydrocharitaceae, mostly tropical species but represented in the United States by three dioecious genera, Elodea, Vallisneria, and Limnobium. The small staminate flowers of Vallisneria, each with three functional stamens, are crowded into a dense head within a sheath composed of three valves. The pistillate flower is solitary and is borne on a very long scape. The three carpels are united with a unilocular ovary which is coherent with the tube of the perianth; i.e., the flower is epigynous. The perianth is three-lobed. The female flower by a rapid growth of the scape rises to the surface of the water, where the expanded stigmas come into contact with pollen. The male inflorescence becomes detached and is floated to the vicinity of the female flower, and the discharged pollen is borne to the stigmas. After pollination the scape becomes spirally coiled and draws the flower beneath the surface, where the fruit completes its development.

All the marine monocotyledons belong to the Helobiales. These include the eelgrass (*Zostera*) and *Phyllospadix* of the Pacific Coast—both belonging to the Potamogetonaceae—and a number of tropical genera, e.g., *Halophila*, *Thalassia*.

ORDER 3. TRIURIDALES

This includes a single small family, Triuridaceae, composed of small saprophytes, destitute of chlorophyll, with minute scale leaves. They are strictly tropical, with representatives in South America and the Eastern tropics. The flowers are usually diclinous and resemble those of some Helobiales; but the development of the embryo is apparently not known, and Engler states that they may perhaps not be monocotyledons. They are, however, tentatively placed next the Helobiales.

ORDER 4. GLUMALES

Two large and very characteristic families, the true grasses, Gramineae (Poaceae) and the sedges (Cyperaceae), represent the Glumales. While the two have many similar structures, they show also very notable differences, which indicate that they are not closely related, but neither shows any very clear indication of near relationships with any other monocotyledons. They are cosmopolitan in their distribution, and play a very important role in the vegetation of nearly every part of the world. The grasses alone have about 500 genera and probably ten times as many species. The largest number of species are tropical, but it is in parts of the temperate zones that they are most important. This is abundantly shown in the prairies and great plains of the central United States, where the grasses dominate the vegetation, with a relatively small admixture of other plants.

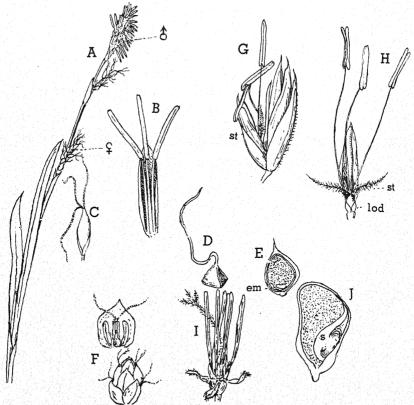


Fig. 307.—A, Carex sp.; &, staminate flowers; Q, pistillate flowers; B, staminate flower; C, pistillate flower; D, ripe fruit of Carex Asa Grayi; E, section of D; F, flowers of Scirpus lacustris; G, spikelet of Dactylis glomeratus; H, single flower of Dactylis; st, stigma; lod, lodicules; I, Bambusa vulgaris; I, grain of maize; s, scutellum (I, from Hackel, after Kunth).

With the drier conditions farther west, the solid turf of the prairies is replaced by bunch grasses intermixed with a larger number of other plants. In tropical regions the grasses may be tall, reed-like species, like the "Alang" grass, Imperata arundinaceae, which quickly covers the cleared areas with an almost impenetrable thicket. There are some aquatic species, like the wild rice (Zizania aquatica), and a few forest species; but as a rule the grasses grow in open spaces, where they hold their own against the most aggressive dicotyledons.

Economically the grasses are the most important of all plants. In temperate climates they furnish the staple food of most herbivorous animals, and all the cereals—rice, wheat, corn, etc.—are grasses. Bamboo and sugar cane also belong to the Gramineae.

The Cyperaceae, including sedges, bulrushes, and a number of less familiar forms, while comprising some 3,000 species, are much less varied than the grasses and are very much less important economically. The largest genera of the Cyperaceae are Cyperus and Carex, which include about a third of the known species. Another large genus is Scirpus, to which the bulrushes belong. Cyperus Papyrus is the Egyptian papyrus. They are often aquatics, like the bulrushes, papyrus, and many sedges, are abundant in boggy sour soils, and are characteristic also of the Arctic and sub-Arctic zones. There are many tropical species, but they play a much smaller role in the vegetation.

The stem in most of the grasses, like that of Equisetum, has hollow cylindrical internodes and solid diaphragms at the nodes. As in Equivieum there is also a notable deposition of silica in the outer tissues. In the sedges the stem is solid and often triangular in section but also has a marked deposit of silica in the cortex and the epidermis.

The leaves in the Glumales are typically elongated, narrow structures, with parallel veins. The leaf base is a sheath, which in the grasses has an appendage, the ligule, and is split; in the sedges the sheath is entire. The leaves are two-ranked in the grasses, three-ranked in the sedges.

Flowers.—The flowers in none of the Glumales have a perianth, and they are enclosed in special chaffy bracts (glumes). Some have both stamens and carpels; in others the flowers are diclinous. In the grasses the hermaphrodite (bisporangiate) flowers are the rule, but sometimes, e.g., in maize, the flowers are diclinous. The "tassel" at the top is composed of the staminate flowers, the ear of the pistillate. The flowers of the grasses are arranged in "spikelets" which consist of a short axis (rhachilla) having at its base usually two bracts or glumes, and from one to several bracts or lemmae, in the axil of which the flower is borne. Between the flower and the rhachilla is another bract, the palea. The latter belongs to the floral axis, the lemma to the rhachilla. Above the latter there

are usually two small bodies, "lodicules," which sometimes have been interpreted as a rudimentary perianth.

The pistil consists of a unilocular ovary containing a single ovule and with two plumose styles. The "silk" of Indian corn consists of the two greatly elongated styles fused into a single filament. The stamens are typically three, but may be occasionally two; in rice (Oryza) there are six and in some of the bamboos a still larger number.

In the Cyperaceae the flowers are similar to those of the grasses, but there is usually a rudimentary perianth composed of bristles or small scales. The stamens, typically three, may sometimes be reduced to a single one. The ovary is unilocular, with a single ovule, with commonly three styles.

The embryo sac in the grasses may show a marked increase in the number of antipodal nuclei. Cannon found more than 36 in Avena fatua at the time of fertilization. Whether or not a similar condition might occur in the Cyperaceae is not known.

The fruit (grain) of the Gramineae is a "caryopsis"; i.e., the seed is completely fused with the tissue of the ovary. The development of the embryo is typical and it is well advanced in the ripe seed. There is a very short suspensor, and the cotyledon is developed from this whole terminal portion of the embryo. As in the Helobiales, the stem apex is lateral. A feature of the older embryo is the "scutellum," serving as a haustorium and usually regarded as the modified cotyledon. Opposite the scutellum there is sometimes a small appendage (epiblast), which has also been interpreted as the cotyledon. Between the scutellum and the epiblast is the stem apex. On germination the root first emerges, followed by the stem apex, which is enclosed in a membranaceous cylinder, the "coleoptile," the first organ to appear above ground.

In the Cyperaceae, the embryo remains small and undifferentiated in the ripe seed, which is filled with endosperm.

ORDER 5. PALMALES

The very natural family Palmaceae includes all the 1,000 or more species of palms, which are especially characteristic of the tropical zones but have a number of genera which extend into the temperate zones. Thus in the United States the palmetto (Sabal Palmetto) is found in the Carolinas, and in southern Florida there are several genera. In southern California a single species, Washingtonia filifera, is found. There are also a number of species in temperate South America, Australia, New Zealand, and South Africa, and a single species, Chamaerops humilis, in southern Europe.

The palms are in most cases trees, sometimes very tall, and greatly

surpassing in size any other monocotyledons. The climbing rattans (Calamus spp.) of the Eastern tropics are said to be the longest of all plants. In the equatorial regions of South America and Indo-Malaya the palms reach their maximum development and constitute a very important element in the forest vegetation.

The crown of leaves reaches its full size before the trunk develops, and the trunk, although it may be 100 feet high, does not increase materially in diameter with age, as it does in *Pandanus*, and the arborescent Liliaceae, like *Dracaena* and *Yucca*. While there is some increase in size between the youngest part of the trunk and the older portions, this is due apparently entirely to the enlargement of the cells of the ground tissue apparently entirely to the enlargement of the cells of the ground tissue between the vascular bundles; there is no formation of new bundles. The irregular swelling of the trunk, such as is so conspicuous in the royal palm (*Orcodoxa regia*), probably is of the same nature; but further investi-



Fig. 308.—Group of palms, Stanford University (photographed by Dr. D. A. Johansen).

gation on this point is needed. A possible exception is the dom-palm (*Hyphaene*) of upper Egypt, where there is a dichotomous branching. Otherwise the trunk is unbranched. Secondary shoots may arise at the base of the trunk—a phenomenon common in some of the smaller palms which grow in clusters.

A section of the trunk, in spite of its size, is essentially like the stem of a typical monocotyledon. Some of the smaller palms have their slender stems armed with long, needle-like spines—e.g., Acrocomia, Astrocaryum, and Calamus.

The edible fruits of some of the palms, like the date and coconut together with their value for furnishing building materials, and fibers, make them, next to the grasses, economically the most important family of plants.

Leaves.—The leaves of the palms are sharply plaited when young, and on unfolding split along the lines of the folds. Two types are found in the mature leaf: fan-shaped, with long petioles, e.g., Sabal and Washingtonia; and pinnate, where the lamina splits into distinct segments, which are separated by the elongation of the rhachis (midrib), resulting in the pinnate form found in the majority of the palms, e.g., Cocos and Phoenix. In one genus, Caryota, the leaves are bipinnate and may perhaps be truly compound.

The leaf base forms a sheath, which may remain attached to the trunk long after the leaves have died. The persistent leaf bases form a rough armor, which completely hides the surface of the trunk except in the basal part. In some palms, like the royal palm (Oreodoxa) and the coconut, the leaf base is a sheath completely surrounding the trunk, and falls off with the leaf, leaving a circular scar on the smooth trunk.

In some of the rattan palms, the rhachis is extended into a slender, whip-like appendage provided with circles of thorns, like claws, by which the slender climbing stems are supported and which also make a thicket of tangled rattans—something to be avoided by the experienced botanical collector.

Root.—The primary root of the young plant has a limited growth and is replaced by numerous secondary roots. Although these may be very stout, they have no secondary increase in size. In a few palms, like the South American Iriartea, there are stilt-roots much like those of Pandanus.

Flowers.—The flowers are borne on branched inflorescences, sometimes of gigantic size. In a few genera, e.g., Corypha, the enormous inflorescence is formed at the apex of the trunk, and the tree dies when the fruit is ripe. In most palms the inflorescences are developed from the axils of the leaves. The inflorescence is enclosed in a number of special bracts (spathes), which sometimes may form a woody sheath enclosing the ripe fruits.

The flowers may be either hermaphrodite or diclinous. The date palms,

Phoenix, are dioecious. In the palmetto, the flowers are hermaphrodite. There are also monoecious genera, e.g., Ceroxylon and Iriartea.

The flower has a perianth, usually of 6 members arranged in two whorls. The outer series being smaller than the inner ones, but both alike in texture, and not conspicuous in color. There are usually six stamens and three carpels, and the flower conforms to the "typical" monocotyle-donous formula. The carpels may be separate or coherent, and often only a single carpel is fertile, so that only a single fruit is produced from each flower. The fruit is generally a berry or drupe (stone-fruit), which may reach a great size, e.g., coconut. The development of embryo sac and embryo is very imperfectly known.

Classification.—Five subfamilies of palms are recognized by Drude. Of these, four are obviously related; but a fifth group, Phytelephantinae, differs much from the other palms, and there is doubt as to their relationship. There are but two genera: Phytelephas, whose seeds yield "vegetable ivory"; and Nipa fruticans, the Nipa palm of the Eastern tropics. It has been thought that the Phytelephantinae might connect the palms and the Pandanaceae, but Drude concludes that this is not warranted, and that in their essentials they are true palms.

Relationships.—It is recognized that the Palmales cannot be connected directly with any of the other orders of the monocotyledons. No members of the lower orders except Pandanus can be called "arborescent," but the section Bambuseae of the Gramineae includes species which rival in

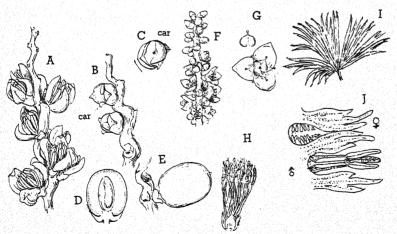


Fig. 309.—A, staminate, B, pistillate flowers of Phoenix canariensis; C, fertilized flower of Phoenix, only one carpel functional; D, section of young fruit; E, ripe fruit; F, part of inflorescence of Erythea edulis; G, single flower of Erythea; H, staminate flower of Phytelephas Rivieri; I, leaf of Carludovica palmata; J, section of inflorescence of Cyclanthus; Q, pistillate flower; C, staminate flower (H-I, from Engler and Prantl).

height the tallest palms. *Dendrocalamus giganteus* may have stems 40 meters in height, although it is true that these giant canes are developed in a single season.

There are certain similarities in structure, however, that might suggest a remote relationship, although these are by no means entirely convincing. The jointed stems and conspicuous leaf sheaths of the bamboos are not unlike the slender trunks of many palms. The large divided leaves of most of the palms are very different from those of any grasses, but the early leaves of the seedling are not very unlike an ordinary grass leaf. The floral structures are not very different, and the caryopsis of the grass might be compared with the drupe of the palm. The smooth hard surface of the bamboo shoot can be matched by that of some of the slender palms, like the rattans, and in both cases this is due to the deposit of silica.

At any rate the grasses seem to show more similarity to the palms than do any other monocotyledons. Both orders are ancient ones, and while it is improbable that either one has been derived from the other the possibility of a remote relationship between them is not inconceivable.

ORDER 6. CYCLANTHALES

Like the Palmales, this order includes but a single family with some 48 species confined to tropical America. There are six genera, some of which are slender lianas with aerial roots but most of which are terrestrial with a short stem or creeping rhizome.

The majority belong to the genus Carludovica, common in the West Indies and South America. They look like small fan-palms. The long-stalked, fan-shaped leaves are divided into two or more parts. The monoecious flowers form a compact spike, like the spadix of the Araceae. The pistillate flower has a rudimentary perianth of four segments, and the four carpels are united into a unilocular ovary with four parietal placentae and numerous ovules. Alternating with the four carpels are four greatly elongated staminodia. The ovary is partly immersed in the spadix. Between the pistillate flowers are groups of four staminate flowers with numerous stamens. The staminate flower has no perianth. The inflorescence is enclosed in several conspicuous white bracts, suggesting the spathe of some of the Araceae. These bracts fall off later. "Panama" hats are made from the leaves of Carludovica.

Another genus, Cyclanthus, has four species. C. bipartitus is common in Trinidad and the Guianas. The leaves are soft in texture, unlike those of the palms, and recall rather the Araceae. There are milk tubes present also. The leaves are bifid, like those of Carludovica. The spadix is subtended by several broad, spathe-like bracts. The flowers are sometimes arranged in a series of closely set, regular rings; or there is a continuous spiral from the base to the apex of the spadix.

Relationships.—The relationships of the Cyclanthales with the other monocotyledons are not at all clear. Carludovica undoubtedly closely resembles the palms in its general habit, but the herbaceous texture and the presence of milk tubes in Cyclanthus suggest the Araceae, and the structure of the fruit is much like that of Freycinetia of the Pandanaceae.

The fruit is radically different from that of the palms, where there is only a single seed in each loculus instead of the numerous ovules in the Cyclanthaceae. It is thus a question whether the Palmales, the Pandanales, or the Arales are most nearly related to the Cyclanthales.

ORDER 7. ARALES

ARACEAE

A large majority of the Arales belong to the Araceae, most of whose species—about 92 per cent according to Engler—are confined to the tropics. Over a hundred genera have been described, but many of these genera are monotypic or have only two or three species. Only a small number are found in the temperate zones. The sweet flag, Acorus Calamus, and Calla palustris occur in both the colder parts of the United States and Canada and in Eurasia; and the former has a very wide distribution in the temperate regions of North America and Eurasia. About a dozen species of Araceae are found in the United States; but only one of these, the Western skunk cabbage (Lysichiton), occurs on the Pacific coast. The same species

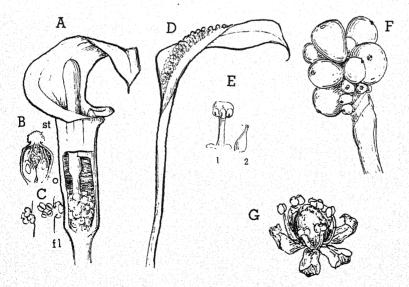


Fig. 310.—A, Arisaema triphyllum, pistillate inflorescence; B, section of pistillate flower; st, stigma; o, ovules; C, staminate flowers; D, E, Spathicarpa sagittaefolia; E, I, staminate flower; E, 2, pistillate flower; F, fruits of Nephthytis liberica; G, flower of Acorus Calamus (G, after Engler).

occurs in Kamchatka. The "Jack-in-the-pulpit" (Arisaema triphyllum) represents a genus of some 50 species, especially developed in eastern Asia. The other eastern American genera are Peltandra, Symplocarpus, and Orontium. The Araceae reach their maximum development in the wet tropics of South America and the East Indies. Of the tropical genera only a very small number are common to the Eastern and Western hemispheres,

Most of the Araceae have broad leaves, which may have a thick midrib with parallel lateral veins, as in the "calla lily" (Zantedeschia); or there may be a reticulate venation much like that of the typical dicotyledons, e.g., Symplocarpus and Pothos. The leaves are often arrow-shaped, and may reach a very great size. The largest leaf is found in Amorphophallus Titanum. The leaf, developed from a huge subterranean tuber, has an erect stalk said to be 3–5 meters in height, with a correspondingly broad, much-divided lamina. True compound leaves are found in Arisaema, Syngonium, and Zamioculcas.

In the species from temperate regions there is usually a subterranean corm or rhizome, from which each season new leaves and flowers are developed. In most tropical species there is a permanent aerial stem, which sometimes may form a short upright trunk; or they may be epiphytes, climbing high into the trees, and developing numerous pendent aerial roots. Some of these climbing aroids with their gigantic leaves, like species

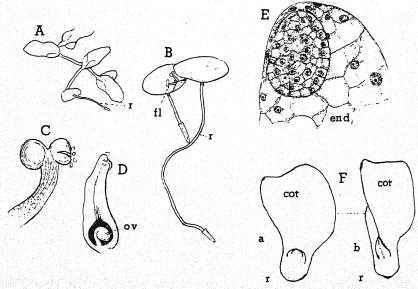


Fig. 311.—A, Lemna trisculca; r, root; B-D, Lemna minor; r, root; C, staminate flower; D, pistillate flower; E, embryo of Lysichiton Kamtchatcense; F, two sections of large embryo of Anthurium cordifolium; cot, cotyledon; r, root.

of *Philodendron* in America and the East Indian *Scindapsus*, are characteristic features of the tropical rain-forest. There are some aquatic species, like the arrow arum (*Peltandra*) of eastern United States and the floating *Pistia stratiotes*, found throughout the tropics of both hemispheres. A striking aquatic species is *Montrichardia arborescens*, a common South American species whose crowded bare stems, crowned with large arrowshaped leaves, form a close palisade fringing the margins of the rivers.

The Araceae are mostly herbaceous, differing thus from the palms and the Pandanaceae and recalling, rather, the Helobiales and Cyclanthus. Characteristic are cells containing needle-like crystals (rhaphides) of calcium oxalate. Milk tubes are also of frequent occurrence.

Flowers.—The flowers usually form a thick spike or "spadix," which in most cases is partly enclosed in an enveloping bract or spathe, which may be very conspicuous. The white spathe of the "calla lily" and the bright red spathes of some species of Anthurium are familiar examples. These are probably associated with attraction of insects. In some species of Amorphophallus the spadix is over a meter in length and the spathe is nearly as long. In these large inflorescences a marked amount of heat is given off when the pollen is shed, and at this time often an extremely offensive odor is developed which seems to attract carrion-loving insects, which presumably are agents in pollination.

In its simplest form, e.g., Aglaonema and Spathicarpa, the flower consists of a single carpel, with a solitary basal ovule, or of a single stamen. In other forms there may be a rudimentary perianth and both stamens and carpels. There are in most cases two or sometimes more carpels united into a compound ovary. The number of ovules varies. Acorus, which differs most from the typical Araceae, has narrow, sedge-like leaves and a naked spadix. The flowers are much like those of some of the higher monocotyledons. There are six perianth segments, six stamens, and usually three carpels. The fruit in the Araceae is often a berry, containing numerous seeds; and the cluster of scarlet berries in Arisaema and some other Aroids is very conspicuous. Engler believes the hermaphrodite flower, like that of Acorus or Anthurium, is the primitive form, and the diclinous flowers, e.g., Spathicarpa and Arisaema, are derivatives; but this conclusion might be questioned.

The development of the embryo sac in the Araceae shows great variation. It may conform to the usually angiosperm type; but there are many variations—sometimes there is a single embryo-sac mother cell, but sometimes a group of such cells, e.g., Arisaema; and more than one embryo sac may begin to develop. There is also great difference in the structure of the embryo sac itself. It may have the typical form; but in some cases, e.g., Lysichiton, there is a marked increase in the number of antipodals, re-

calling in this respect Sparganium. In Nephthytis and Aglaonema the writer found extraordinary variability, which was difficult to explain except as possibly abnormalities induced by growth under artificial conditions in cultivation.

The endosperm in all the Araceae that have been examined is septate from a very early stage and completely fills the embryo sac, a condition very much like that in *Peperomia*, one of the lower dicotyledons. As in *Peperomia* also the embryo sac may remain relatively small and the outer tissue of the ovule serve as perisperm; but this is not the case in all the Araceae.

The embryo in the ripe seed may be very small, or it may when mature completely fill the embryo sac. The earliest divisions are like those in most monocotyledons. There is no evident suspensor; and the differentiation of the organs, even in the large embryo, takes place at a late period. In the absence of a suspensor, and in its form, there is a suggestion of the embryo of the grasses and of Sparganium. The greater part of the embryo is made up of the large flattened cotyledon, which might be compared with the scutellum of the grass embryo. The stem apex is inconspicuous and is enclosed by the base of the cotyledon. In Lysichiton the primary root is lateral; but in Anthurium cordifolium, as in the typical monocotyledons, it is basal.

LEMNACEAE

The second family of the Arales, the Lemnaceae, includes several genera of minute floating plants in which the plant body is an undifferentiated frond, which produces buds that remain attached for a time but may become separated and form new individuals. In Lemna each flattened shoot develops a single root; in Spirodela several roots are formed; and in Wolffia, the smallest of all the spermatophytes, the oval plant body is rootless. W. arrhiza is less than 2 millimeters in diameter.

The branches emerge from pockets. In Spirodela a rudimentary leaf is formed at the base of the young shoot; but this is not formed in the other genera.

The flowers in Lemna consist of a single stamen or a carpel containing a single ovule. Two staminate and one pistillate flower form a minute inflorescence contained in a cleft or pocket on the margin of the frond.

RELATIONSHIPS OF ARALES

Like the palms and the grasses, the Arales form a sharply defined order with no very evident indications of relationship with any other group. The characteristic spadix is comparable with the inflorescence of the Pandanaceae and some palms, which also may have spathe-like bracts. It is, however, doubtful that these resemblances indicate any real relationship.

Engler believes that the Arales may have originated from some Helobiales, especially the Potamogetonaceae. The inflorescence of Potamogeton does suggest a spadix, and some of the Arales are floating aquatics, e.g., Lemna and Pistia, while other aquatic genera occur, e.g., Acorus, Peltandra, and Montrichardia, and most of the species grow where there is abundant moisture. It is therefore not improbable that the Araceae have been derived from aquatic ancestors. There are some interesting similarities in structure between the Araceae and the dicotyledonous order, Piperales. The structure of the stem in Peperomia is like that of a simple monocotyledon and the leaves of many of the Piperaceae closely resemble those of Araceae; and this is true also of the inflorescence, and to some extent of the ovule and the embryo sac. In the family Saururaceae, Anemopsis has the spadix-like inflorescence subtended by white bracts, which might be compared with the showy spathe of an aroid. Whether or not these resemblances between the Araceae and Piperales indicate any real relationship cannot of course be definitely answered.

The seven orders of the monocotyledons discussed in the preceding pages comprise the "spiral" types of Engler. They show many evidences of being more primitive than the four orders of the "cyclic" families, which include the predominant petaloideous monocotyledons of the existing floras. The spiral types show much less definiteness in the floral structures. They are often diclinous and are often destitute of a perianth and have a variable number of stamens and carpels.

While there are three large orders, viz., Glumales, Palmales, and Arales, the total number of species in the seven orders is only about one-third of that in the four cyclic orders. In the Glumales and the Palmales and a few of the Arales there is a tendency toward a definite number of the floral organs. The flower often shows the definite trimerous structure of the "typical" monocotyledons.

In the four cyclic orders—Farinales, Liliales, Orchidales, and Scitaminiales—the flowers are for the most part pentacyclic and trimerous, i.e.: perianth, 3–3; stamens, 3–3; carpels, 3. The perianth in the majority is petaloideous and there are many special modifications of the flowers, mostly associated with the visits of insects. This culminates in the Orchidaceae, the largest of all the families of angiosperms, almost equaling in number of species all the other monocotyledons.

ORDER 8. FARINALES

Eleven families and about 2,000 species belong to the Farinales. The lower families have inconspicuous flowers, recalling the Glumales, to which perhaps they are related. The perianth may be absent or it may be composed of membranaceous segments. The flowers may be diclinous or her-

maphrodite. The inflorescence is often enclosed in bracts, suggesting the glumes of the grasses, and many of them resemble the grasses and sedges in habit.

In the more specialized types, like *Tradescantia*, the Bromeliaceae, and *Pontederia*, the perianth segments, especially the inner ones, are showy, like those in the Liliales. Thus the Farinales may be said to connect the more primitive orders with the Liliales. How far the resemblances are due to real relationships and how far the result of parallel development in the Farinales and Liliales is not easy to determine. The most marked difference between the two orders is in the seeds. In the Farinales the endosperm is always starchy and is "mealy" in texture. The embryo is small in most families, being largest in the Bromeliaceae.

The Farinales are poorly represented in temperate North America, and the few species are mainly confined to the Atlantic States. The majority of the species are tropical; but some of the simpler families, e.g., Restionia-

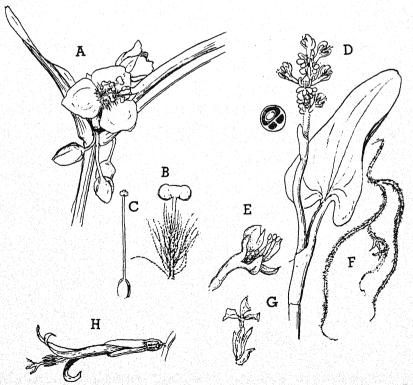


Fig. 312.—A, Tradescantia virginica; B, stamen; C, pistil; D, Pontederia cordata; E, flower of Pontederia; F, Tillandsia usneoides; G, flower of Tillandsia; H, flower of Bilbergia Bakeri (H, after Engler and Prantl).

ceae and Centrolepidaceae, are practically confined to the South Temperate Zone, especially South Africa and Australasia. The Flagellariaceae, a small tropical family, is found in the islands of the South Seas, with a single endemic species, *Joinvillea adscendens*, in Hawaii.

In the families Commelinaceae and Bromeliaceae there is a differentiation of the perianth into calyx and corolla, the latter sometimes being very showy. The Commelinaceae are represented by several species of Tradescantia in the United States. The Bromeliaceae, much the largest family of the order, is exclusively American but has relatively few representatives outside the tropics. The "Spanish moss" (Tillandsia usneoides) and several other species of Tillandsia are found in the Gulf States, especially Florida; but it is in Central and South America that they reach their maximum development. One important cultivated plant, the pineapple, is a bromeliad, and a number of showy species of Bilbergia and some others are occasionally seen in cultivation. Many species are epiphytes, and some of the large terrestrial species of Puya, with long narrow stiff leaves, recall Yucca or Dracaena. The broad, sheathing leaf bases may serve as reservoirs for water or humus. The flowers are often showy, but often much more conspicuous are the bright pink or scarlet bracts surrounding the inflorescence. The flower may be either hypogynous or epigvnous and the fruit either a dry capsule or a berry.

The Pontederiaceae have a single representative in eastern United States—Pontederia cordata, the pickerelweed. In Pontederia the perianth is tubular and is zygomorphic, like the flower of Gladiolus and some other Iridaceae. In the Southern States the water hyacinth, Eichornia crassipes, a member of the same family introduced from tropical America, has become a serious pest.

The most specialized of the Farinales belong to the small family Philydraceae, in which the flower is strongly zygomorphic and suggests the Orchidaceae. Like most of the Orchidaceae, also, only a single functional stamen is present. The Farinales thus show a tendency in floral development not unlike that of the next order, the Liliales.

ORDER 9. LILIALES

Included in the Liliales are many common flowers—lilies, tulips, hyacinths, Iris, Narcissus, and many others. These are often looked upon as the typical monocotyledons. The flowers have five cycles of generally three members. The two outer whorls forming the perianth are as a rule alike. In a few genera, e.g., Trillium, there is a definite green calyx and a petaloid corolla. This recalls the same condition in Tradescantia and many Bromeliaceae. Within the Liliales there is every gradation between the radially symmetrical (actinomorphic), hypogynous flowers of a lily, and

the epigynous, zygomorphic flowers of many Amaryllidaceae and Iridaceae. In the latter, one set of stamens is suppressed.

The fruit of the Liliales is most commonly a dry capsule; but in some cases, e.g., Asparagus and Convallaria, it is a pulpy berry. The seed has abundant endosperm and a small embryo. The endosperm cells are generally thick-walled, with oily contents; less commonly the endosperm is starchy, but it does not have the "mealy" consistency found in the Farinales.

The Liliales are mostly herbaceous plants, inhabitants of the temperate zones, producing each season annual flowering shoots from perennial subterranean bulbs, corms, or rhizomes. In warmer regions they may be perennials, sometimes becoming small trees, like the Yuccas of the Southwestern States and the Dracaenas, the Aloes, and the Cordylines of the Old World. A small number, e.g., Smilax and Dioscorea, are climbers.

Over 5,000 species are included in the Liliales, and these are placed by Engler in nine families: Juncaceae, Stemonaceae, Liliaceae, Amaryllidaceae, Haemadoraceae, Velloziaceae, Taccaceae, Dioscoreaceae, Iridaceae.

In a recent discussion of the monocotyledons Hutchinson recognizes 28 orders, raising many families, e.g., Liliaceae and Amaryllidaceae, to ordinal rank.

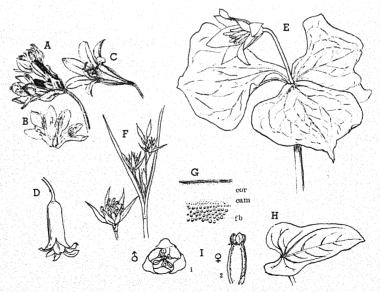


Fig. 313.—A, B, Brodiaea capitata; C, B. laxa; D, Polygonatum commutatum; E, Trillium erectum; F, Juncus sp.; G, section of outer part of stem of Yucca aloifolia; cor, cortex; cam, cambium; fb, vascular bundles; H, leaf of Dioscorea Batatas; I, c, staminate flower; Q, pistillate flower (H, I, after Pax, in Engler and Prantl).

FAMILY I. JUNCACEAE

The members of the rush family, Juncaceae, are sedge-like plants with insignificant flowers, recalling those of the sedges or grasses, or the simpler members of the Farinales, e.g., Flagellariaceae.

The genus Juncus includes a large majority of the species widespread over the temperate and colder parts of the world. The flower has the typical lily-structure, except that one member of the outer perianth cycle is suppressed. The perianth members of the insignificant flowers are greenish or brownish, with six stamens (sometimes reduced to three) and three carpels. The Juncaceae are often regarded as reduced forms, but it is possible they represent the most primitive members of the order and indicate a point of contact of the Liliales and the lower Farinales. The Juncaceae also have starchy endosperm, but it is solid and not mealy, like that of the Farinales.

FAMILY II. STEMONACEAE

A small family, mostly tropical, with a single representative, *Croomia* pauciflora, in Florida and Georgia. They differ from the typical Liliales in having the floral organs in twos instead of threes.

FAMILY III. LILIACEAE

The lily family is one of the largest among the monocotyledons, with over 2,500 described species. They are cosmopolitan but reach their greatest development in the temperate regions. In the Northern Hemisphere they are represented by some of the most beautiful flowers, such as lilies, tulips, hyacinth, *Scilla*, *Fritillaria*, and *Hemerocallis*, all familiar garden favorites.

The type genus, Lilium, with possibly 100 species, is confined to the North Temperate Zone, except for a few species in the mountains of northern India, and the Philippines. There are about a dozen species in Pacific North America and several in the Atlantic States. The finest species, like L. auratum and L. regale, from Japan and China, are common in cultivation. California is very rich in Liliaceae. Besides the handsome native lilies, there are numerous species of the beautiful mariposa lilies (Calochortus), of Brodiaea, Erythronium, Yucca, and other showy Liliaceae. South Africa and Australia have some characteristic Liliaceae, some of which, like Agapanthus, Aloe, and Kniphofia, are cultivated in California and other mild climates.

In regions with a cold or dry season the Liliaceae generally develop bulbs, tubers, or rhizomes, which are dormant during the resting period and develop new flowering shoots each year.

FAMILY IV. HAEMADORACEAE

Nearly all the members of the small family Haemadoraceae belong to the Southern Hemisphere, but a single monotypic species, *Lachnanthes tinctoria*, is found near the Atlantic Coast of the United States. Most of them are found in Australia and South Africa, and several occur in South America. The inconspicuous flowers are like those of the Liliaceae but have only three stamens.

FAMILY V. AMARYLLIDACEAE

The Amaryllidaceae are evidently closely related to the Liliaceae, from which they differ in having an inferior ovary, and, a good many of them, zygomorphic flowers. They are mostly tropical or subtropical and are not very well represented in the United States. In the South the large white flowers of Hymenocallis, a common marsh plant, are conspicuous, and Zephyranthes, with pink or white flowers, often seen in cultivation, is a native of the southern Atlantic States. In the extreme Southwest and in Mexico are species of Agave, one of which, the common "century plant," is sufficiently familiar. Some of the Amaryllidaceae are common in cultivation. Among these are the many types of Narcissus, the snow drop (Galanthus), and species of Amaryllis, Hippeastrum, Crinum, and Alstroemeria.

FAMILY VI. VELLOZIACEAE FAMILY VII. TACCACEAE

These two small families, whose relationships are obscure, are essentially tropical in their distribution. The Velloziaceae are with few exceptions confined to Brazil, but some species occur in tropical and subtropical Africa. In Vellozia there are always more than six stamens.

The relationships of the Taccaceae are especially doubtful, and it has even been held that they are intermediate between monocotyledons and dicotyledons. The leaves are often very much dissected, recalling those of certain Araceae. There are about ten species (all but one belonging to Tacca). The majority are Asiatic, but a few species are found also in South America.

FAMILY VIII. DIOSCOREACEAE

Nine genera are included in the Dioscoreaceae, but a very large majority of the species belong to *Dioscorea*, with some 150 species, mostly tropical. A few species are found in the temperate zones, and a single one, *D. villosa*, wild yam, is common in eastern United States. *D. Batatas* is the edible yam of the tropical countries.

The yams are climbing plants, with heart-shaped reticulate veined leaves and inconspicuous, mostly dioecious, flowers. The perianth is sixparted; the staminate flower has six stamens; and the trilocular ovary is

inferior. The vascular bundles of the stem are arranged in a single circle much like those of the typical dicotyledons. The embryo has the stem apex developed from the terminal segment of the embryo, as it is in Zaninichellia, a condition intermediate between that in most monocotyledons and the typical dicotyledons. There is in most cases a subterranean rhizome or tuber; but the edible yam is said to be a root tuber.

FAMILY IX. IRIDACEAE

Next to the Liliaceae, the Iridaceae are the most numerous of the Liliales, and also the most specialized. Like the Amaryllidaceae the flowers

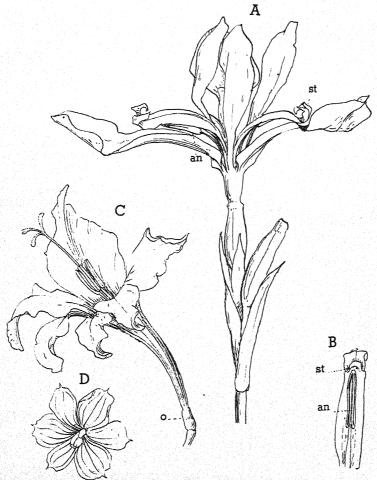


Fig. 314.—A, Iris versicolor; B, stamen and stigma of the same; C, Gladiolus sp.; o, inferior ovary; D, Sisyrinchium bellum.

are epigynous, but there are only three stamens. The flower may be actinomorphic, with all the perianth segments alike (Sisyrinchium, Ixia), or it may be strongly zygomorphic (Freesia, Gladiolus). In Iris the inner perianth segments differ in form from the outer ones; and a similar condition is found in Tigridia. In most of the Iridaceae the leaves are sharply folded ("equitant") and the leafy shoots with their two-ranked leaves are flattened. They are mostly herbaceous, with perennial root stocks, corms, or bulbs, and are most abundant in the warm temperate regions and relatively rare in the colder parts of the North Temperate Zone. Iris, however, is exclusively boreal in its distribution. This genus and Crocus are especially numerous in the Mediterranean countries. The Cape region of Africa, the home of a great variety of Iridaceae, has furnished many choice garden flowers, e.g., Gladiolus, Ixia, Freesia, Sparaxis, and Watsonia.

The great majority of the American species belong to *Iris* or *Sisyrin-chium*. The latter is one of the least specialized members of the family, while *Iris* is the most specialized, with a highly elaborate apparatus for

cross-fertilization.

ORDER 10. SCITAMINIALES

The Scitaminiales are almost exclusively tropical forms, sometimes of almost tree-like proportions. The leaves are large—sometimes gigantic—and species like the large bananas, and the "traveler's tree" (Ravenala), are among the most striking of all tropical plants. In nearly all of them the growth of the shoot is limited, and is completed with the formation of the terminal inflorescence. In the bananas (Musa) the stout trunk is formed entirely from the sheathing bases of the leaves; but in Ravenala and some species of Strelitzia there is a permanent trunk and the inflorescences are borne in the leaf axils. In the other genera there is a fleshy rhizome or tuber from which the aerial shoots are developed. The leaves have a broad lamina with thick midrib and lateral parallel veins. The leaf base is a conspicuous sheath.

The simplest type of flower is found in the Musaceae, and may be compared to that of the Amaryllidaceae. The ovary is inferior, and the flower has six perianth leaves and six stamens. In the other more specialized families the perianth is never petaloid, and there is often a reduction in the number of stamens. Only one is fertile, the others being sterile staminodia, some of which are petaloid, and take the place of a showy corolla.

The fruit may be a pulpy "berry," e.g., banana; but more often, as in Canna, it is a dry capsule. The seed is generally large, with the small embryo surrounded by the endosperm; but the embryo sac is relatively small, and the endosperm is supplemented by perisperm derived from the tissue of the nucellus. In the cultivated banana the seeds are abortive.

Classification.—There are four families: Musaceae, Zingiberaceae, Cannaceae, and Marantaceae. Of these the first two are predominant in the Old World, and the last two are mostly American.

FAMILY I. MUSACEAE

The type of the family, Musa, includes such important plants as the cultivated bananas and plantains (M. Sapientum and M. paradisiaca), of which there are innumerable varieties. These have been cultivated from the earliest times, and are usually seedless. There are, however, many wild species in the Eastern tropics. M. textilis of the Philippines yields Manila hemp. The flowers in the bananas are monoecious, and they are subtended by large bracts, which sometimes are highly colored.

Ravenala differs in habit from Musa, having a permanent stem and the large two-ranged leaves spread out like a fan. Two species are known, R. madagascariensis, the "traveler's tree," and a second species from northern South America. Two other genera, Strelitzia from South Africa and Heliconia from tropical America, belong to the Musaceae. The former has large showy flowers. In S. reginae, often cultivated in California, the outer perianth leaves are brilliant orange and the inner ones, which enclose the stamens and pistil, bright blue. Heliconia has the bracts subtending the inflorescences brilliantly colored red and yellow. The Heliconias are very conspicuous features of the American tropics.

FAMILY II. ZINGIBERACEAE

This is much the largest family of the order, and is represented by many genera and species distributed in both the Eastern and Western tropics but much more abundant in the former. Some of them, like the cultivated ginger, Zingiber officinalis, and Hedychium coronarium, "wild ginger," common in Hawaii, have become naturalized in many tropical regions.

The flowers are sometimes very showy, and superficially resemble some of the orchids. The perianth is differentiated into calyx and corolla, but these are not conspicuous. Only a single fertile stamen is developed, and the others when present form staminodia, one of which is modified into a showy labellum or lip which recalls the lip of the orchid flower. There is also a suggestion of the orchids in the close apposition of the style with the filament of the solitary fertile stamen. These resemblances, however, are evidently not true homologies.

Only four genera are found in America, and two of these, *Costus* and *Renealmia*, occur also in West Africa. There are also species of *Costus* in tropical Asia and Australia.

FAMILY III. CANNACEAE

The only genus is Canna, sufficiently familiar in American gardens. It was supposed that the genus was strictly American, but it has been claimed that several species are indigenous in West Africa and eastern Asia. One species, C. flaccida, is native from Florida to South Carolina, and others are found throughout tropical America. The perianth has two whorls, which are relatively inconspicuous. There are four or five large petaloid staminodia and a single fertile stamen, which is also petaloid in appearance. The endosperm in the seeds is largely replaced by perisperm.

FAMILY IV. MARANTACEAE

The Marantaceae are second to the Zingiberaceae in number of species. In contrast to the latter, they are predominantly American. Structurally the flowers resemble the Zingiberaceae—in the development of petaloid staminodia and the reduction of the functional stamens to a single one. They are especially abundant in Brazil; and one genus, Thalia, has two species in southern United States, and one in Paraguay and Uruguay. There are also a small number of Marantaceae in West Africa and the Eastern tropics. Maranta arundinacea furnishes the "arrow root" of commerce, and some species are cultivated for their handsome variegated foliage.

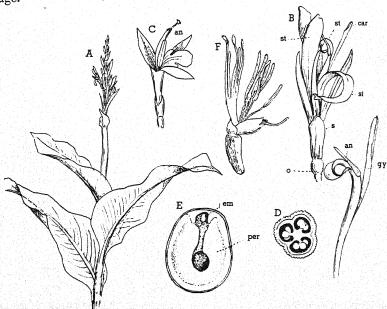


Fig. 315.—A, Canna indica; B, flower of Canna; st, staminodia; car, style and stigma; fertile stamen, an, and stigma, gy; C, Zingiber officinalis; D, section of ovary in Canna; E, seed of Canna; em, embryo; per, perisperm; F, flower of Musa ensete (C, after Berg-Schmidt in Engler and Prantl; F, after Peterson).

THE RELATIONSHIPS OF THE SCITAMINIALES

In the most recent review of the order in Engler and Prantl, Die Natürlichen Pflanzenfamilien (2d ed., Vol. 15a), Winkler concludes that the Scitaminiales represent a natural group which cannot be connected directly with any of the Liliaceae but shows evident similarity to the Amaryllidaceae. many of which show the characteristic zygomorphy of the Scitamineae and the inferior ovary. Winkler also indicates that they may be said to occupy a position intermediate between the Amaryllidaceae and the Orchidaceae. The Musaceae are recognized as the least modified forms, the zygomorphy being less pronounced, and the free functional stamens 5-6 in number. The reduction of the functional stamens to a single one, in the Zingiberaceae, and the development of a staminodium into a labellum, which in form and position closely resembles that of an orchid, are apparently assumed by Winkler to be indications of a real relationship. The Musaceae, according to Winkler, are connected with the Zingiberaceae through Orchidanthera, a member of the subfamily Lowioideae. A comparison of the latter with some of the Orchidaceae, e.g., Arundina, shows some significant correspondences.

The Cannaceae, while undoubtedly related to the other Scitaminiales, form a very clearly differentiated family, most nearly related to the Marantaceae.

Whether or not the obvious similarities in the appearance of the floral structures of the Zingiberaceae and Orchidaceae really indicate a genetic relationship may be questioned. These resemblances might be purely homoplastic.

At present no forms are known which are intermediate in the seed characters between the Scitaminiales and Orchidales. The large seeds of the former, with the development of endosperm and perisperm, are in marked contrast with the minute seeds of the orchids.

ORDER 11. ORCHIDALES

Except for the small family Burmanniaceae, the members of the order may be referred to a single family, Orchidaceae, the largest family of the angiosperms. Over 17,000 species of orchids have been described, about half the total number of all the known monocotyledons. They are, however, rarely sufficiently numerous as individuals to become a dominant factor in the vegetation. Although there are extraordinary devices for insect pollination, and the seeds are very numerous, they do not seem to have been especially successful in the struggle for existence.

The orchids are cosmopolitan, and while they reach their maximum development in the tropics a good many species occur in the temperate zones, and some may even be found as far north as Alaska and Labrador in America, and Scandinavia in Europe.

The Orchidaceae include the most specialized monocotyledons, and show a greater range of habit than any other order. In the cooler regions they are terrestrial, and this is true also of many tropical species; but very many of the latter are epiphytes. Where there is a marked dry season, the epiphytic orchids often have the leaf bases developed into "pseudobulbs," serving for water storage. Aerial roots are also a marked feature of some epiphytic species. Such characteristic genera as Neottia and Corallorrhiza are saprophytes growing in humus soils. These have no chlorophyll, and the leaves are reduced to scales. These saprophytic orchids are dependent for their growth upon certain mycorrhizal fungi, and apparently all orchids require the presence of this mycorrhiza in the soil and in the tissues of the roots or rhizomes, thus recalling the Ophioglossaceae.

The flower.—With few exceptions the flowers are strongly zygomorphic, with one of the inner perianth segments forming a conspicuous lip or labellum. The stamens in the majority of species are reduced to a single fertile one, which is united with the pistil to form the "column" or "gynostemium." In some of the lower forms, there may be two perfect stamens or even three.

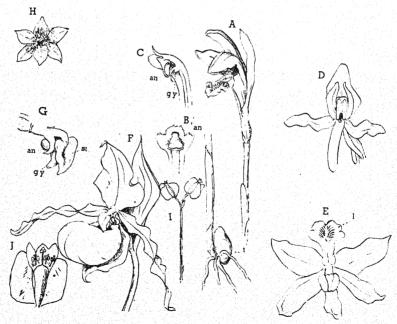


FIG. 316.—A, Arethusa bulbosa; t, tuber; B, gynostemium of Arethusa; C, section of gynostemium; an, anther; gy, stigma; D, Habernaria flava; E, Calopogon pulchellus; I, lip; F, Cypripedium pubescens; G, gynostemium of Cypripedium; st, staminodium; gy, stigma; H, Thelymitra ixioides; I, I, Burmannia biflora (H, from Pfitzer, after Blume; I, I, after Britton and Brown).

The Orchidaceae are divided into two sections, the Diandrae and the Monandrae, the latter containing a very large majority of the species. In the former there are two functional stamens, or, in a very few cases, three; in the Gynandrae there is but a single one.

The simplest and probably the most primitive of the orchids is a small subfamily, Apostasieae, found in Australia and the Malayan region. The flowers are almost actinomorphic, no definite lip is developed, and the stamens are incompletely fused with the style. In *Apostasia* one of the three stamens forms a sterile staminodium; in *Neuwiedia* all three stamens are functional. The structure of the flower might be compared with some of the Iridaceae.

Most of the Diandrae belong to the subfamily Cypripedilineae, of which the "lady's slippers," Cypripedium, are the most familiar representatives. The native species are among the showiest of the wild orchids. The strongly zygomorphic flower has the posterior petal developed into the inflated saccate lip, which, as in most of the orchids, owing to a twist in the inferior ovary, appears to be on the anterior side of the flower. Three stamens are present; two belonging to the inner cycle are functional and are lateral; the third stamen, belonging to the outer cycle, forms a conspicuous staminodium. The pollen in the Diandrae is granular.

FAMILY I. MONANDRAE

The Monandrae have but a single fertile stamen, completely fused with the style to form the column. The flowers are with few exceptions markedly zygomorphic, and the lip is often greatly modified and extremely conspicuous. A frequent modification is the presence of a long hollow spur, forming a nectary, one of the common structures associated with insect pollination. Occasionally, e.g., in the Australian Thelymitra ixioides, the lip differs but little from the other perianth segments, and the flower seems to be practically actinomorphic. Another exceptional case is seen in the American Calopogon, where the ovary is not twisted and the labellum retains its primitive posterior position. In the Monandrae the pollen coheres in definite waxy masses or "pollinia," which in most cases can be removed only with insect aid. There are many extraordinary devices by which this is brought about.

At the time of pollination the ovules are still in a rudimentary condition, and there may be a considerable interval between pollination and fertilization of the ovules. The inferior ovary is unilocular, with three parietal placentae bearing very numerous ovules. The seeds are extremely small, with no endosperm and a very minute embryo. The Orchidales are therefore sometimes called Microspermae.

In size the orchids range from some very minute epiphytic species,

only a few centimenters in length, to a few reaching a length of 3-4 meters. One of these giants is *Grammatephyllum speciosum* from the Malay Archipelago. From the base of the leafy shoots, some 3-4 meters in length, develop the stout upright flowering stems, two meters or more in height, bearing a mass of large brown and yellow flowers. It is sometimes called the "tiger orchid." The species of *Vanilla* climb by means of root tendrils.

Many tropical orchids have long been cultivated and have given rise to numerous beautiful hybrids—some the results of crosses between two or even three distinct genera. A few of the commoner cultivated genera are Cattleya, Laelia, Odontoglossum, and Oncidium from the American tropics, and Vanda, Dendrobium, Phalaenopsis, and Cymbidium from the Indo-Malayan regions.

In the United States the Orchidaceae are best represented in the Eastern and Southern states. Some of these have showy flowers, especially species of Cypripedium, Habenaria, Pogonia, Arethusa, and Calopogon. In Florida a number of West Indian types are found, especially species of Epidendrum.

FAMILY II. BURMANNIACEAE

This family includes about sixty species of small plants which it has been thought may be intermediate between some of the Amaryllidaceae, like Hypoxis, and the Apostasieae, which are regarded as the most primitive of the Orchidaceae. The Burmanniaceae are often saprophytic and occur in both the Eastern and Western tropics. Two species of Burmannia are found in the Gulf States. Burmannia has three stamens, but in some of the other genera there are six. The seeds are small but nevertheless have a small amount of endosperm: the embryo, like that of the Orchidaceae, is minute.

PHYLOGENY OF THE MONOCOTYLEDONS

Are the monocotyledons, as a whole, a primitive or a derivative group? It is most commonly believed that they have been derived from dicotyledons and that their predominantly herbaceous character is due to the adoption to an aquatic or geophilous habit, the latter resulting from cold or dry conditions.

Since the greater part of the monocotyledons are tropical and especially abundant in the humid areas, this explanation is not entirely satisfactory. The geophilous habit of most of the Scitamineae and Araceae, and of many Orchidaceae, so characteristic of the wet equatorial forests, hardly harmonizes with this theory. It is quite as likely that this herbaceous character is primitive, inherited perhaps from some filicinean ancestors. The Filicineae are predominantly herbaceous and geophilous, and the existing heterosporous genera, especially *Isoetes*, which show interesting suggestions of a

possible relationship with the monocotyledons, are either aquatic or amphibious. The preponderance of monocotyledons in the tropics suggests

that they originated under similar conditions. A study by Bews of the flora of South Africa, a region which geologically is very old, indicates it includes a larger proportion of primitive types than do the forests of cooler regions, which he believes originated secondarily from tropical ancestors. If this view is correct, the many monocotyledons, especially in the forest margins and shores of rivers and lakes, might well be ancient forms and not secondary types as now believed by many

It is agreed that during the Jurassic and Early Cretaceous, when it is botanists. supposed angiosperms first became prominent, a much more uniform climate prevailed than at present, presumably warm if not tropical. This would support Bews' conclusion that the angiosperms originated under tropical conditions; and the predominance of monocotyledons today in the tropics might indicate that they are relict forms, rather than secondary ones and that their simpler structure is not the result of reduction from dicotyledonous ancestors.

In view of our present knowledge it may be assumed that the monocotyledons are as old as the dicotyledons but do not form a single closed phylum. Some of the order, e.g., Palmales, Glumales, and Arales, are very clearly circumscribed and show little indication of genetic relationship with any other major group. Coulter proposed three main stocks, represented by the Pandanales, the Helobiales, and the Glumales. With the Pandanales he associated the Palmales and the Synanthales; with the Helobiales, the Arales; and with the Glumales, the remainder of the monocotyledons. Such a conclusion is merely tentative, and is open to numerous objections.

The higher orders—Farinales, Liliales, Scitaminiales, and Orchidales are probably related. At the bottom of the scale are such families as the Flagellariaceae and the Juncaceae, which might possibly connect with the Glumales. The Liliales are connected through the Amaryllidaceae, and perhaps the Iridaceae, with the Orchidales. The highly specialized Scitaminiales may perhaps through the Musaceae connect also with the Amaryllidaceae but have diverged from the main line and are not related to the Or-

chidales.

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CHAPTER XXV

ANGIOSPERMS—DICOTYLEDONS: APETALAE

The dicotyledons, in number of both species and individuals, are preeminently the modern plant type. They show a much greater range of structure than is found in the monocotyledons; but some of the simpler dicotyledons, like the Ranales (buttercup family), the peppers, and the water lilies, show such evident structural resemblances to some of the lower monocotyledons, like the Helobiales and the Arales, as to indicate a possibly real, if remote, relationship.

The theory that the dicotyledons are the older group, from which the monocotyledons have been derived, is questionable; and the theory that the simplest flowers, like those of the Naiadaceae and the grasses, or many apetalous dicotyledons, are reduced from petaloideous ancestors ignores entirely the fossil evidence, which indicates that these "reduced" forms

are among the oldest-known angiosperms.

The relative numbers of the monocotyledons and the dicotyledons, as well as the generally much less specialized character of the former, perhaps might be interpreted as indicating that they are a relict group, rather than a relatively recent one derived from the dicotyledons.

The angiosperms, as they now exist, probably represent a number of independent phyla—some monocotyledons, some dicotyledons—i.e., they

are polyphyletic.

The dicotyledons show an extraordinary range in size, structure, and habit. Some are small herbaceous annuals living but a few weeks or months; other are giant trees living for centuries. Aquatics are less common than in the monocotyledons. Among these aquatics are species of *Utricularia* and *Myriphyllum*. The curious Podostemonaceae are aquatic thallose plants with no differentiated structures except the flowers. The mangroves live with their roots actually in salt water.

"Xerophilous" types, like the cacti, some Euphorbias, sagebrush, and many other desert plants, are common among the dicotyledons. Parasites and saprophytes are well represented, and epiphytes and climbers abound. Of the parasites, dodder (Cuscute) and mistletoe (Viscum, Phoradendron) may be mentioned, and there are a few "root parasites," some completely parasitic without chlorophyll, like the cancerroot (Orobanche), others partial parasites, i.e., Castilleia and Gerardia. The most extreme parasitism is exhibited by the Rafflesiaceae of the Eastern tropics. The plant lives

within the body of the host, like a fungus, and is reduced to fungus-like filaments, but develops flowers, sometimes of enormous size, which break through the cortical tissue of the host and expand outside. In short, among the dicotyledons may be found practically every type of plant structure.

Except for a few forms, like the palms, the screw pines, and arborescent Liliales, trees are unknown among the monocotyledons. Dicotyledons make up the forests everywhere, except where conifers predominate. Many dicotyledonous families are composed exclusively of woody shrubs or trees; e.g., the oak family (Fagaceae), the maples (Aceraceae), and the magnolias (Magnoliaceae). The dicotyledons, as a rule, are more gregarious than the monocotyledons, except for a few families, like the grasses. In most regions, especially in the temperate zones, dicotyledons constitute the major part of the dominant floras.

EMBRYO SAC

The development of the embryo sac is of the usual angiospermous type. With relatively few exceptions it has the typical egg apparatus—two polar nuclei, three antipodal cells. The most marked departure from this type is found in *Peperomia* and *Gunnera*, where there are 16 nuclei and the endosperm nucleus is formed by the fusion of several nuclei.

Embryo.—The typical dicotyledonous embryo has two opposite cotyledons, between which is the stem apex. Below the cotyledons, the axis ("hypocotyl") merges gradually into the primary root ("radicle"). In most forms, at least, a definite suspensor is developed.

There is in a number of cases a more or less complete suppression of one of the cotyledons, a condition to some extent intermediate between

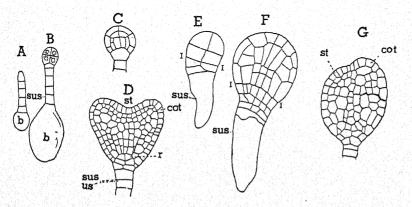


Fig. 317.—A-D, development of embryo in Capsella; E, F, embryos of Senecio aureus; G, embryo of Zannichellia palustris, a monocotyledon; the stem apex, st, is terminal, not lateral (E, F, after Mottier).

that of the monocotyledons and the dicotyledons, perhaps to be compared to the terminal stem apex and lateral cotyledon in Dioscorea and Zannichellia. Examples of these "pseudo-monocotyledons" are Cyclamen, Abronia, Ranunculus, and Ficaria. The Ranales also afford some other examples of structures suggestive of the monocotyledons. Thus Delphinium nudicaule has the two cotyledons united into a tube, with the plumule at the bottom, very much as in many monocotyledons. In Podophyllum there is a similar condition, and its first foliage leaf has a bilobed lamina, resembling closely a pair of united cotyledons.

As in the monocotyledons the degree of development in the ripe seed varies much. In most cases, the organs of the young sporophyte are well advanced, and in the "exalbuminous" seed may completely fill it. In some families, i.e., Ranunculaceae and Papaveraceae, the embryo is very small and may even be quite undifferentiated, and the endosperm fills nearly

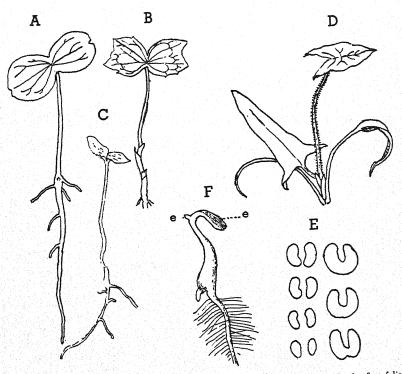


Fig. 318.—A, seedling of Podophyllum peltatum, the cotyledons united; B, the first foliage leaf of the second year; C, seedling of Delphinium nudicaule, with united cotyledons; D, seedling of Victoria regia, showing the first leaves; E, series of cross sections of the cotyledonary region of Podophyllum; F, seedling of Abronia umbellata, one cotyledon abortive (A, B, after Holm; D, from Goebel, after Trecul; E, after Mottier; F, after Hill).

the whole seed. In some of the lower families, e.g., Piperaceae and Nymphaeaceae, abundant perisperm largely replaces the endosperm, recalling the Cannaceae, the Zingiberaceae, and some of the Araceae.

The cotyledons may differ but little from the later leaves, but often they have a quite distinct form. In exalbuminous seeds, where the food materials are stored in the greatly thickened cotyledons, as in the legumes, and stone fruits, they may remain within the seed until the food materials are exhausted, when they withdraw from the seed coat, develop chlorophyll, and for a time function as foliage leaves.

ANATOMY

The stem.—The stem apex has no single apical cell, but there can be recognized a meristematic region in which the initials for the three tissue systems can be recognized. The epidermal layer, dermatogen, covers the apex, and beneath this is the periblem or primary cortex. Inside the periblem is the plerome, forming the central axis of the shoot. The limits of the plerome are not always readily recognized, and the origin of the "procambium" layer from which the vascular bundles develop is not always perfectly certain.

In a typical herbaceous dicotyledonous stem there is below the epidermis a cortical layer of chlorophyllous cells, the outer ones forming a more or less definite hypoderma, much as in the monocotyledons. The central region is the medulla or pith.

In a transverse section of the stem, the vascular bundles form a circle surrounding the pith and are enclosed in a common endodermis, formed from the innermost layer of the cortex. In some anomalous forms, like *Peperomia*, *Podophyllum*, and *Nelumbo*, the bundles are scattered through the ground tissue of the stem very much as in the typical monocotyledons.

In the hypocotyl of the seedling, the vascular bundles are separate; but very soon a cambium zone is formed connecting the cambium of the individual bundles, thus making a continuous cambium cylinder composed of "fascicular" and "interfascicular" cambium. As the woody stem increases in size, the primary cortex disappears and is replaced by secondary bark formed from an active meristem (periderm) developed in the cortex.

The general structure of the stem in the dicotyledons thus resembles that of the conifers. The structure of the wood is much like that of the conifers, but there are also true vessels, which are absent from coniferous wood. In the phloem are sieve tubes, elongated "companion cells," and bast fibers.

While the activity of the cambium usually results in regular concentric growth rings, there are a good many exceptions. Sometimes a second cambium ring is developed inside the ring of wood (*Tecoma radicans*); or each

primary bundle may be surrounded by a separate cambium forming several masses of wood surrounded by a common cortex. This is especially characteristic of some woody climbers or lianas. There are numerous other variations.

The leaf.—The leaves of the dicotyledons are much more varied than those of the monocotyledons, although they never equal in size the leaves of the palms, the bananas, and some other monocotyledons. In general

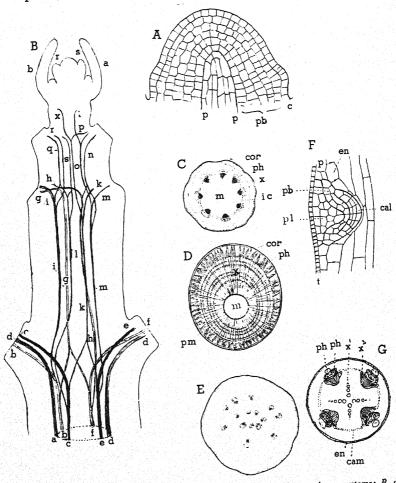


Fig. 319.—A, stem apex of Hippuris vulgaris, showing the primary tissue systems; B, diagram showing arrangement of the vascular bundles in Clematis viticella; C, section of the hypocotyl of Ricinus communis; m, pith; cor, cortex; x, xylem; ic, interfascicular cambium; hypocotyl of a branch of Tilia americana, with six annual growth rings; E, section of stem of Peperomia trinervis; F, rootlet developing from the pericycle of a root of Amarantus othlorostachys; G, diagram showing secondary thickening in a dicotyledonous root (A, after De Bary; B, after Nägeli; F, after Van Tieghem).

the leaf has a definite petiole, sometimes with stipules at the base, and a broad lamina with midrib and a complex system of reticulate veins. The leaf margin may be entire, or it may be variously cut or lobed; or the leaf may be pinnately or palmately compound. Further division of the leaf lamina results in the "decompound" leaves. In some parasitic species the leaves are reduced to scales, and in some xerophytes, as well as in some other cases, the leaves are either absent or are reduced to small scales and the chlorophyll is restricted to the cortex of the shoot, which may, as in some of the cacti, become flattened and leaf-like.

In regions with a marked winter most of the woody dicotyledons shed

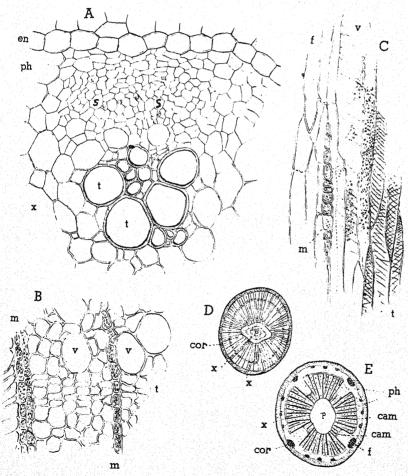


Fig. 320.—A, vascular bundle from stem of Tropoeolum majus; B, cross section of wood of Tilia americana; C, longitudinal section of the wood; D, E, anomalous stem structure in woody climbers; D, Tecoma radicans; E, Bignonia sp.

their leaves and the leaf buds are protected by closely set, thick scale leaves. The deciduous habit is probably secondary; it is found also in tropical and subtropical regions where there is a prolonged hot dry period.

The root.—The primary root of the dicotyledons, like that of the conifers, is a continuation of the hypocotyl, and may persist as a permanent taproot. With the growth of the plant there is developed an extensive root system which, like the woody stem, develops cambium, and a similar secondary increase in size.

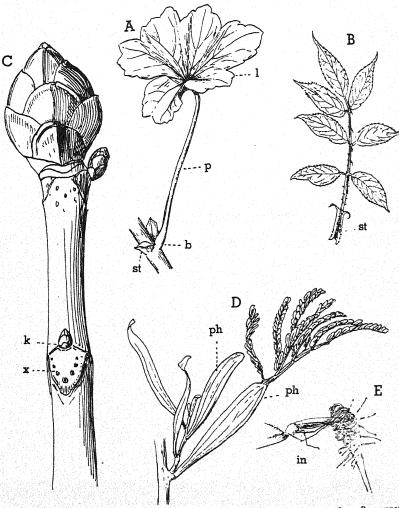


Fig. 321.—A, leaf of Pelargonium sp.; l, lamina; p, petiole; st, stipules; B, compound leaf of a rose; C, horse chestnut, with bud scales; k, lateral bud; x, leaf scar; D, Acacid melanoxylon, with phyllodia, ph; E, leaf of Drosera capturing an insect.

FLOWERS

The flowers of the dicotyledons show much the same trend in their evolution as the monocotyledons, but exhibit a much greater range in structure. Some of the simplest forms have no floral envelope and may even be reduced to a single stamen or carpel. These simple flowers are usually monoecious or dioecious. Some of these simpler floral types are with little question really primitive; but there are others which are probably reduced from more specialized ones. The majority of the dicotyledonous flowers have conspicuous floral envelopes, both calyx and corolla; but there are a good many monochlamydeous genera where the corolla is absent. Sometimes in these the calyx is petaloid and often is mistaken for a sympetalous corolla; Daphne and Mirabilis are examples of such petaloid calyces.

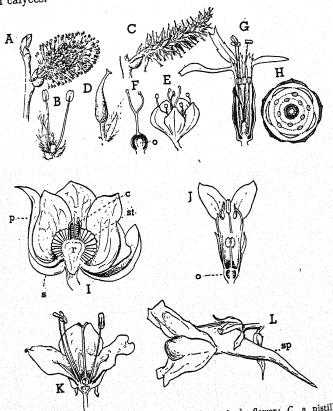


Fig. 322.—A, staminate catkin of a willow; B, a single flower; C, a pistillate catkin; D, a pistillate flower; E, monochlamydeous flower of Polygonum sp.; F, pistil of the same; G, choripetalous flower of Silene virginica; H, floral diagram of Silene; I, hypogynous apocarpous flower of Asimina triloba; c, carpels; st, stamens; J, perigynous flower of Houstonia purpurea; o, ovary; K, actinomorphic sympetalous flower of Hydrophyllum appendiculatum; L, zygomorphic sympetalous flower of Linaria vulgaris; sp, spur.

The Dialypetalae, or Choripetalae, include those families which typically have flowers with definite calyx and corolla. The sepals are commonly green and may be regarded as morphologically true leaves; the petals, however, are probably not modified leaves but are transformed stamens (sporangiophores). The familiar phenomenon of double lowers and the occurrence of petaloid staminodia, comparable to those of Canna and the Zingiberaceae, are evidence of the nature of the petals. In certain flowers, i.e., Eucalyptus and other Myrataceae, Thalictrum, Acacia, and others, the corolla is either wanting or inconspicuous, the stamens forming the showy part of the flower.

The flowers of the Ranales, one of the lower orders, in many cases show an indefinite number of parts, in both the perianth and the stamens and carpels. The same is true in the Magnoliales, which are sometimes included in the Ranales. These flowers are also generally apocarpous, i.e., have the carpels entirely separate. In floral structure the apocarpous Ranales recall the monocotyledonous Helobiales, with which they may perhaps be remotely related.

With the increasing specialization, there is a reduction in the number of stamens and a tendency to a cohesion of the perianth with the floral axis and the ovary, such as was noted in some of the monocotyledons. The apocarpous gynoecium becomes syncarpous, forming a compound pistil. The number of functional carpels is most commonly less than the stamens. Cohesion of the sepals with the margin of the floral axis is common, resulting in a tubular or cup-shaped calyx; where the petals are coalescent, there results the "gamopetalous" corolla, characteristic of the Sympetalae, which include a majority of the dicotyledonous species.

Where the ovary is entirely free, or "superior," the flower is hypogynous; where it is more or less coherent with the floral axis and the base of the corolla, it is "inferior" and the flower is perigynous or epigynous.

The most specialized of the dicotyledons are the Sympetalae. The corolla may be actinomorphic, as in the morning-glory, Campanula, or it is zygomorphic, as in the Labiatae and the Scrophulariaceae. In the zygomorphic flowers there is usually a reduction in the number of stamens to 4 or 2. Zygomorphy also occurs, but less frequently in the Choripetalae, e.g., Delphinium, Tropoelum, and Viola. Zygomorphy, and the accompanying modifications in the stamens and pistil, are associated with insect pollination.

While in the majority of the dicotyledons the floral parts are in fours or fives, there are many exceptions; and in some of the more primitive families, e.g., Magnoliaceae, Nymphaeaceae, Berberidaceae, and Anonaceae, the flowers are typically trimerous and recall the monocotyledons.

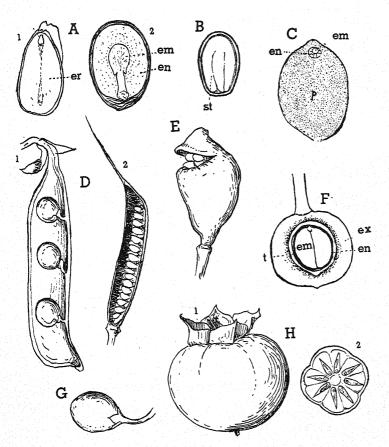


Fig. 323.—A, albuminous seeds of Jeffersonia diphylla and Diospyros virginiana; en, endosperm; B, exalbuminous seed of Capsella; C, seed of Peperomia, endosperm replaced by perisperm, p; D, I, legume of pea; D, 2, follicle of Aquilegia; E, fruit of Jeffersonia diphylla; F, section of young drupe of a cherry; G, berry of Solanum dulcamara; H, I, fruit (berry) of Diospyros virginiana; H, 2, section of the ovary.

Some genera of the Ranunculaceae and Polygonaceae, i.e., Coptis, Hydrastis, Rumex, and others, show a similar trimerous structure.

The fruit and seeds of the dicotyledons show all the types known in the angiosperms.

CLASSIFICATION OF THE DICOTYLEDONS

The relationships of the numerous orders of the dicotyledons are very uncertain, and any arrangement adopted must be at present somewhat tentative. There is much difference of opinion as to the scope of the orders. Hutchinson recognizes 76 orders, Wettstein only 39.

Two main divisions of the group are generally recognized, viz., Choripetalae, or Archichlamydeae, and Sympetalae—Metachlamydeae. Within the Choripetalae are two categories: Monochlamydeae, including the so-called "Apetalae"; and "Dialypetalae." The Apetalae include several orders which differ greatly from the typical Choripetalae and include what are probably the most primitive members of the dicotyledons. For the most part they show but little resemblances to the higher orders, and perhaps should be removed from the Choripetalae.

Most of the Apetalae are shrubs or trees and include many important forest trees, especially in the temperate zones. Among these are oaks, beech, elm, walnut, hickory, willows, and poplars. Some of these are among the earliest angiospermous fossils, occurring in the Cretaceous rocks, indicating that they are among the most primitive of the living members of this class. This makes it extremely likely that the simple floral structures of these Apetalae are primitive and not secondary.

Engler recognizes the following apetalous orders: (1) Verticillatae; (2) Piperales; (3) Salicales; (4) Myricales; (5) Balanopsidales; (6) Leitneriales; (7) Juglandales; (8) Fagales; (9) Urticales; (10) Proteales; (11) Santalales; (12) Aristolochiales; (13) Polygonales. To these might be added (14) Garryales.

ORDER 1. VERTICILLATAE

This order contains but a single genus, Casuarina, with some twenty species, mostly Australian, but with several in the South Pacific islands, the Malay Archipelago, and tropical Asia. They are trees or shrubs, the slender jointed leafless twigs recalling the sterile shoots of Equisetum. The flowers are monoecious, with the staminate flowers in whorls in the axils of the leaf sheaths. The female inflorescence recalls the cone of a conifer. The staminate flower consists of a single stamen, the pistillate of two carpels. Casuarina shows no satisfactory evidence of relationship with any other dicotyledons. Wettstein would derive the family directly from the Gnetales—especially the Ephedraceae—to which it certainly bears a striking superficial resemblance; and this is also true of the development of the embryo sac and the floral structure. Two species, C. equisetifolia and C. stricta, are sometimes planted in California.

ORDER 2. PIPERALES

The Piperales are for the most part tropical; some are herbaceous forms, others shrubs or climbers. These simple flowers have no perianth, and most of them are hermaphrodite but are sometimes diclinous. They usually form dense spikes, much like the spadix of some of the Araceae. The leaves also suggest the Araceae. There are three families: Piperaceae,

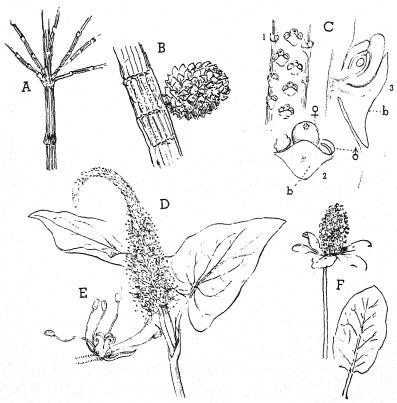


Fig. 324.—A, Casuarina equisetifolia; B, ripe seed cone of Casuarina; C, Peperomia blanda; C, I, spike with flowers; C, 2, a single flower; C, 3, section of ovule; b, subtending bract; D, Saururus cernuus; E, single flower of Saururus; F, Anemopsis californica, the spike subtended by petal-like bracts (F, after Jepson).

Saururaceae, and Chloranthaceae. The first includes the great majority of the species, the two principal genera, *Piper* and *Peperomia*, having many species throughout the tropical regions. *Piper-nigrum* furnishes commercial black pepper. *Peperomia* is notable for the 16-nucleate embryo sac and the monocotyledonous stem structure. There are about four hundred species, mostly delicate herbaceous plants, many of them epiphytes.

The flower in *Peperomia* has two stamens and a single carpel; the ovary is unilocular and contains a single ovule. The fruit is a berry; the minute embryo sac is embedded in the endosperm, but the embryo sac is small and is surrounded by abundant perisperm. The seed thus resembles that of the Scitaminiales.

The Saururaceae are perennial herbs found in the temperate part of North America and eastern Asia. Two species, Saururus cernuus, of the Eastern States, and Anemopsis californica, from California, are American. The third genus, Houttuynia, is Asiatic. The two latter have the spike of flowers subtended by several white bracts, so that the inflorescence resembles the flower of an Anemone. A comparison might perhaps also be made with the inflorescence in the Araceae.

The third family, Chloranthaceae, is a small family of tropical and South Temperate species. There are three genera: Chloranthus, Ascarina, and Hedyosma. The seed differs from that of other Piperales in having abundant endosperm.

ORDER 3. SALICALES

There is but a single family, Salicaceae, with two genera, Salix and Populus. This family is essentially a North Temperate one. All of the poplars and nearly all of the willows belong to the Northern Hemisphere. They are dioecious, the flowers in catkins. The staminate flower has from two to many stamens; the ovary is unilocular but with 2-4 parietal placentae. Populus and Salix occur fossil from the Lower Cretaceous.

ORDER 4. MYRICALES

The single family, Myricaceae, has but a single genus, Myrica, which is widely distributed. They are shrubs or small trees, having an aromatic fragrance. The flowers are monoecious or dioecious. The staminate flower is much like that of the Salicaceae, the pistillate flower with a single carpel. The unilocular ovary has a single erect, basal ovule, much like that of the Piperaceae. The wax myrtle, M. cerifera, the sweet fern, M. asplenifolia, and two others are found in the Atlantic States, and two on the Pacific Coast.

ORDER 5. BALANOPSIDALES

Balanops is the sole representative of this order. It is found only in New Caledonia, and its relationships are doubtful. Balanops is a tree or shrub, with dioecious flowers, the staminate in catkins, the pistillate solitary, surrounded by an involucre, the whole not unlike the flowers of an oak. Engler concludes that the Balanopsidales are perhaps intermediate between the Salicales and the Fagales.

ORDER 6. LEITNERIALES

The small family Leitneriaceae, with two species from the Gulf States, makes up this order. They are shrubs, with erect catkins of inconspicuous flowers. They are dioecious. The staminate flowers have no perianth, and consist of stamens, subtended by a bract, much like *Populus*. The pistillate flowers have a perianth of several irregular sepals; the ovary is unilocular with a single ovule.

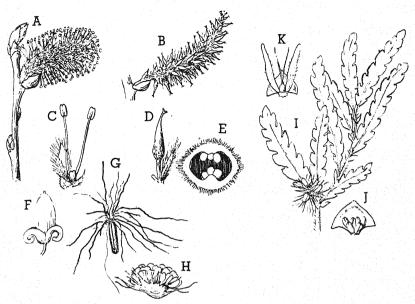


Fig. 325.—A, B, Salix sp.; C, staminate flower of Salix; D, pistillate flower; E, section of ovary; F, G, seeds; H, staminate flower of Populus trichocarpa; I, Myrica (Comptonia) asplenifolia; J, staminate; K, pistillate flowers (I-K after Britton and Brown).

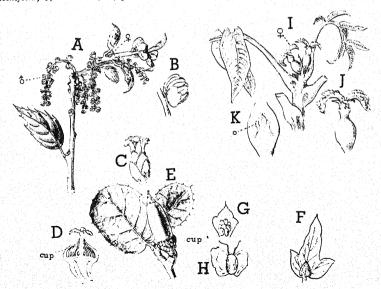


Fig. 326.—A, Quercus agrifolia; \mathcal{O} , staminate flowers; \mathcal{O} , pistillate flowers; B, staminate flower; C, pistillate flower; D, section of pistillate flower; E, ripe acorn; C, cupule; E, ripe fruit of C arpinus; E, staminate flower of E, fruit of E alba; E, E, pistillate flowers; E, pistillate flowers; E, pistillate flowers; E, section of ovary.

ORDER 7. JUGLANDALES

The only family here, Juglandaceae, is represented in the United States by several species of walnuts (Juglans) and hickory (Carya). They are large trees with pinnate leaves. They are monoecious, the staminate flowers in pendent catkins, the pistillate flowers solitary or in small groups. The staminate flowers have several stamens, each flower subtended by a bract. The pistillate flowers have an inferior ovary, and in Juglans have a perianth composed of four small petals. There are two conspicuous styles, but the ovary is unilocular with a single erect basal ovule. The fruit is a drupe, the husk or pericarp being formed from the outer portion of the ovary and the adherent calyx. In the hickory the pericarp splits into four valves. The shell of the nut is formed from the endocarp, the inner part of the pericarp.

The Juglandaceae are restricted to the warmer portions of the Northern Hemisphere, especially in North America and eastern Asia. In the latter area are several other genera, e.g., *Engelhardtia* and *Pterocarya*.

ORDER 8. FAGALES

The Fagales include two very important families of trees, the Betulaceae and the Fagales. To the first belong the birches (Betula), the alders (Alnus), and the hornbeam (Carpinus). Representatives of the Fagaceae are the beech (Fagus), the oaks (Quercus), and the chestnuts (Castanea). The two families include a large part of the important trees of the northern deciduous forests and rank first as hardwood timber trees. The Fagales are almost exclusively northern types. In the Southern Hemisphere the only genus is Nothofagus, the Southern beech, characteristic of the colder portions of the South Temperate Zone, New Zealand, Australia, and subantarctic South America.

The largest genus is *Quercus*, especially well represented in North America. Species extend also into the mountains of Mexico and Central America. Most of the American oaks are deciduous, but in the Southern States and in California are a number of evergreen species like the Southern live oak (*Q. virginiana*) and the Californian live oak (*Q. agrifolia*). In California there is found the so-called tanbark oak, a species differing from the typical oaks, and referred to another genus, *Lithocarpus*, which is otherwise restricted to southeastern Asia, extending to the Moluccas.

The flowers of the Fagaceae are almost always monoecious. The staminate flowers are in pendent catkins, and much like those of the walnuts. The pistillate flower is solitary, with an envelope or involucre of imbricated scales. In the oak these form the cup of the acorn. The ovary is inferior. In the oak, the ovary is usually trilocular, with two ovules in each loculus; but only one seed as a rule matures. In the beech and the chest-

nut the involucre forms the spiny husk, and more than one seed may mature.

In the Betulaceae both staminate and pistillate flowers are in catkins, and there is much less difference between them than in the Fagaceae.

ORDER 9. URTICALES

Of the three principal families included in the Urticales, two, Ulmaceae and Moraceae, are trees or shrubs, while the Urticaceae are for the most part herbaceous. The insignificant flowers are usually diclinous, but perfect (hermaphrodite) flowers may occur in the Ulmaceae. There are a simple perianth, several stamens, and in most cases a single carpel, with a single ovule. The elms (Ulmus) are characteristic trees of the Northern Hemisphere. Two other genera, Celtis and Planera, occur in the eastern United States. A single species of Celtis is the only member of the family on the Pacific Coast. Other species are found in the tropical and subtropical regions, and other genera, i.e., Trema, are found only in the Southern Hemisphere. In the elms, the fruit is winged, a "samara," and in Celtis it is berry-like.

The mulberry family, Moraceae, is a very large one including numerous genera of mostly tropical trees and shrubs. The genus *Ficus*, besides the edible fig, *F. carica*, includes many species of tropical trees, some of them of gigantic size, like the banyan trees, *F. indica*, and others.

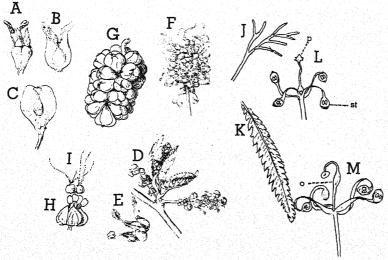


Fig. 327.—A, B, flowers of Ulmus campestris var. suberosa; C, fruit (samara) of Ulmus; D, Morus alba, staminate inflorescence; E, individual staminate flower; F, pistillate inflorescence; G, ripe fruits; H, staminate flower of Utrica sp.; I, pistillate flowers of hop; I, leaf of Grevillea thelymanniana; K, leaf of Banksia serrata; L, flower of Hakea nitida; M, Lomatia sp. (J-M, from Engler and Prantl).

These usually begin life as epiphytes, the seed germinating on the branch of a tree and sending down aerial roots, which finally reach the ground and may coalesce to form a single enormous hollow trunk or, in many, may form a forest of separate trunks.

The milky sap characteristic of the Moraceae contains rubber, which is obtained commercially from several species, e.g., Ficus elastica and Castilloa elastica.

In the mulberry (Morus) the individual pulpy fruits are crowded together forming a structure much like a blackberry; in others, like the breadfruit, Artocarpus, and the Osage orange (Maclura), the fruits are completely coalescent, forming with the fleshy receptacle a "pseudocarp" or "syncarp." In the fig the enlarged apex of the shoot forms a hollow receptacle on the walls of which are borne the individual flowers and later the seed-like fruits.

Among the most characteristic small trees of the American tropics are species of *Cecropia* with jointed stems and long-stalked, large, peltate leaves, somewhat like those of the castor bean.

Forming a small subfamily of the Moraceae, the Cannabineae include a few herbaceous species, which lack the milky juice of the typical Moraceae. Hemp (Cannabis) and hop (Humulus) are the best-known representatives.

Like the Cannabineae, the third family of the Urticalea, the Urticaceae, are mostly herbaceous species. The great majority are tropical, but a few like the nettles (*Urtica*) belong to the temperate zones. Another genus, *Parietaria*, is a cosmopolitan weed.

The inconspicuous flowers of the Urticaceae are much like those of the Moraceae, having usually a perianth comprised of several small sepals with an equal number of stamens, and a unilocular ovary with (usually) a single basal ovule. Some of the family, like the common nettles, have stinging hairs which, especially in the tropical tree nettles (*Laportea* spp.), cause excessively painful stings. Many of the Urticaceae yield excellent textile fibers. The most important of these fiber plants, *Boehmeria nivea*, furnishes "ramie."

ORDER 10. PROTEALES

All of the Proteales may be referred to the single large family Proteaceae, with nearly one thousand species. The family is a highly specialized one, showing no clear evidence of relationship with any other order. Unlike most of the Apetalae, the flowers are often very conspicuous, and it is evident that they are adapted to cross-pollination by insects and probably in some cases by hummingbirds or the honey-sucking birds of South Africa and Australia.

The Proteaceae are almost always shrubs or trees, the latter sometimes of large size. They are especially developed in Australia, where more than half of the species are found, and in South Africa. In South America, there are about fifty species, and there are also some twenty-five species in the Eastern tropics. In America a few species reach Central America. All of the American genera, except Euplasia, are represented also in Australia.

A number of species, mostly Australian, are often cultivated in California. Of these, *Grevillea robusta*, a large tree with very showy orange-yellow flowers, is the most conspicuous. The South African silver tree, *Leucadendron argenteum*, is also sometimes grown in the warmer districts.

The Proteaceae reach their greatest development in Australia, where they are a very important element in the vegetation and include many very striking species. Among these are species of *Grevillea*, *Hakea*, *Banksia*, and, perhaps the showiest of all, *Telopia speciosissima*, the "Waratah" of New South Wales, whose clusters of scarlet flowers surrounded by large brilliant red bracts suggest a double peony. *Protea* and *Leucadendron* are the largest genera in South Africa. Most of the South American species belong to the genus *Roupala*, found in the tropical zone. In Chile are several species of Proteaceae, one of which, *Embothrium coccineum*, is a small tree with very showy scarlet flowers.

For the most part they are adapted to regions with marked wet and dry seasons, such as southern Australia and the Cape region of Africa. The evergreen leaves are thick and may be entire or the margins variously lobed or serrate. In *Grevillea* and some others the leaves are decompound. With very few exceptions the flowers are hermaphrodite. The perianth is composed of four sepals, which may be separate but more often are united into a tubular perianth resembling a sympetalous corolla; these separate later, exposing the stamens and the pistil. The latter is sometimes raised on a pedicel. The unilocular ovary may have a single ovule, but there may be many. The fruit is a capsule or a stone fruit.

ORDER 11. SANTALALES

The Santalales are more or less pronounced parasites whose relationships are not at all clear. They are probably reduced forms. Wettstein associates them with the Proteaceae. The most important families are the Santalaceae, the sandalwood family, and the Loranthaceae, which includes the mistletoes.

The Santalaceae are mostly tropical or subtropical trees or shrubs, but some are herbaceous, e.g., Comandra—small root parasites with several species in the United States. Sandalwood is derived from several species of Santalum, which grow in the South Pacific regions and in Asia. Two species, however, are native to Hawaii, and another genus, Exocarpus, most of whose species are Australian, is also present in Hawaii.

The flowers in the Santalaceae are typically hermaphrodite but by abortion of the stamens or carpels may sometimes be diclinous. The perianth is 4–6 parted, and may be inconspicuous or petaloid. The stamens are the same in number as the sepals. The ovary is inferior and unilocular. The ovules are imperfectly developed, having no integument. In some of the Loranthaceae the ovules are even less evident and are fused with the tissue of the ovary wall. Several embryo sacs may form in this mass of tissue.

The Loranthaceae are mostly parasites on the branches of trees. Two genera, *Phoradendron* and *Arceuthobium*, are the only representatives of the family in the United States. The former is the American "mistletoe," and has green leaves, so that it is a half-parasite. *Arceuthobium* is strictly parasitic, and has no chlorophyll. The European mistletoe (*Viscum*) does not occur in America but is represented by another species in Hawaii. The family is a large one, mostly confined to the tropics. Some species of *Loranthus* have very showy flowers, in some cases showing indications of a division of the perianth into calyx and corolla.

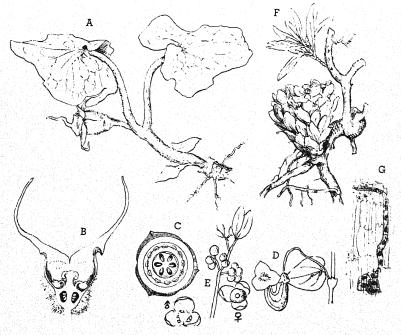


Fig. 328.—A-C, Asarum Canadense; D, Aristolochia macrophylla; E, Phoradendron flavum; S, staminate flower; P, pistillate flower; F, Cytinus hypocistus, parasitic on root of Cistus; C, fungus-like body of Rafflesia Patma, within the tissue of the host (D, E, after Britton and Brown; F, G, after Solms-Laubach).

Probably to be associated with the Santalales are four other families, viz.: Myzodendraceae, with a single genus Myzodendron from southern Chile; Grubbiaceae, three species of Grubbia, from South Africa; Olacaceae, a tropical family of trees and shrubs with numerous representatives in both hemispheres. Balanophoraceae, a family of extreme parasites, are mostly tropical, but some are subtropical. They are all root parasites and quite destitute of chlorophyll. Engler believes they are also probably related to the Santalaceae.

ORDER 12. ARISTOLOCHIALES

The Aristolochiaceae, the principal family in the order, show no evidence of relationship with any other dicotyledons. A large majority are species of *Aristolochia*, a cosmopolitan genus. These are mostly woody climbers, one of which, *A. macrophylla* (Dutchman's pipe), a native of eastern United States, is common in cultivation. Several other species also are found.

The flowers are sometimes very large, e.g., A. gigas. The calyx (perianth) is tubular and usually bent, the margin expanded into a corolla-like limb. The inferior ovary is usually 6-celled, with many ovules. The flowers are insect-fertilized and some of them have a very offensive odor, apparently attractive to carrion-feeding flies.

The only other American genus is Asarum, "wild ginger," of which there are several species, both in the Eastern States and on the Pacific Coast.

The other families associated with the Aristolochiaceae are Rafflesiaceae and Hydnoraceae, parasites of the most pronounced type, and so modified that their relationships are somewhat problematical. They are, however, generally placed next the Aristochiaceae.

The Hydnoraceae are root parasites like the Santalaceae. In the Rafflesiaceae, the vegetative structures are reduced to an irregular thallose body entirely within the tissues of the host, behaving much like the mycelium of a fungus. The flowers break through the cortical tissue of the host, and expand outside. The type genus, Rafflesia, has several species in Java, Sumatra, and the Philippines. R. Arnoldi, from Sumatra, is the largest flower known, sometimes being a meter in diameter. All species of Rafflesia are parasitic on species of Cissus.

There are other Rafflesiaceae in the tropics, and one species, *Pilostylis Thurleri*, is said to probably occur as a parasite on Leguminosae in southern California. Except for a single species of *Prosopanche* in Argentina, the Hydnoraceae contain only about half a dozen species of *Hydnora*, confined to tropical and southern Africa and Madagascar.

ORDER 13. POLYGONALES

All of the Polygonales may be included in the large cosmopolitan family, Polygonaceae, which is best developed in the North Temperate Zone. The large genus *Polygonum* includes the common weeds—"smartweed," "knotgrass," and some others. *Rumex* is represented by the "dock" and the "sheep sorrel." In the West are numerous species of *Erioganium*, some of which differ from most of the order in having a woody stem. Of cultivated plants, the rhubarb (*Rheum*) and buckwheat (*Fagopyrum*) are familiar examples. The leaves usually have sheathing stipules (Ochreae) and in some species of *Rheum* reach a very large size.

The flowers are generally hermaphrodite, but there may be diclinous forms due to abortion of the stamens or pistil. The perianth has 3-6 lobes, which may be either foliose or petaloid. The stamens are more numerous than the sepals. The unilocular ovary is superior, with a single basal ovule. The fruit is a "nutlet" or "achene."

The structure of the pistil and the leaves suggests the Piperaceae, and indicates a possible remote relationship between the Piperales and the Polygonales. More evident relationship is indicated between the Polygonales and the Centrospermae, one of the lower orders of the Dialypetalae.

ORDER 14. GARRYALES

Among the characteristic shrubs of the coastal region of California is the genus Garrya, which is confined to southwestern United States, Texas, California, and Mexico, with a single species in Jamaica. They are shrubs or small trees, with entire opposite leaves and long pendent catkins, bearing either staminate or pistillate flowers on separate plants. The flowers are borne in the axils of conspicuous bracts. The staminate flowers have four sepals and four stamens and are in groups of three, subtended by a common bract. The pistillate flower is solitary, with inferior unilocular ovary, containing two ovules. The inflorescences suggest at once a relationship with such Amentaceae as the Salicaceae or the Betulaceae. Wettstein places the Garryales between the former and the Juglandales. They are more generally placed near the Cornaceae; but it seems more likely that they really are more nearly related to the Amentales.

RELATIONSHIPS OF THE APETALAE

It is generally agreed that the Casuarinaceae are among the most primitive of the Apetalae, but their relation to the other orders is very uncertain. They are regarded by Wettstein as an entirely isolated order derived directly from the Gnetales, but this view is not generally accepted.

Of the remaining orders, it seems most likely that those with diclinous

flowers are the older types, and those with the staminate and pistillate inflorescences alike are the most primitive. Thus the Betulaceae would be older than the Fagaceae, and *Pterocarya* than the Juglans.

The Proteales, with the Santalales, are considered by Wettstein as forming a closed phylum; and the Salicales, the Batidales, the Aristolochiales, and the Piperales are isolated orders, of very uncertain relationships.

The Myricales, both by their floral structure and their geological history, indicate that they represent very old types. The floral structures of the Garryaceae would indicate that they also belong near the base of the Apetalae.

The predominance of basal ovules in so many Monochlamydeae may also indicate that this is a primitive character. Wettstein also cites the presence of vascular strands in the ovular integument of some of the Monochylamydeae as an indication of a derivation from some gymnosperm stock, where this character is found.

The Proteaceae, the Loranthaceae, and the Aristolochiaceae, which often have showy flowers, are indirectly adapted to pollination by insects and probably birds, which indicates that they are more recent types than the anemophilous Amentaceae; but there is no clear evidence of any relationship with the more specialized Dialypetalae. A possible relationship with some of the lower Dialypetalae is indicated in some of the Apetalae. Thus the Piperales have some resemblance to the Centrospermae, and also, as already pointed out, may have a remote relationship with the monocoty-ledonous Arales.

Wettstein, in his diagram showing the phylogeny of the angiosperms, indicates that from the Urticales or from some related stock several phyla of Dialypetalae have been derived. These phyla are represented by the Centrospermae, the Hamamelidaceae, and the Tricoccae (Euphorbiales).

CHAPTER XXVI

ANGIOSPERMS—DICOTYLEDONS: CHORIPETALAE, DIALYPETALAE

The second series of the dicotyledons, the Dialypetalae, typically have the perianth composed of two distinct parts—calyx and corolla. But there are many exceptions, especially in the less specialized orders; and the lines between the Monochlamydeae, the Apetalae, and the Dialypetalae are very vague. Two orders of the latter, especially the Centrospermae and Ranales (Polycarpicae), show obvious resemblances, and probably relationships, on the one hand with the Polygonales and on the other with the monocotyledonous Helobiales, the monocotyledons, as already stated, being considered by many botanists to be derived from dicotyledonous ancestors of the ranalean type. It seems much more likely, however, that the monocotyledons represent several independent phyla derived from protangiosperms. The resemblances may be homoplastic; or the two orders, Ranales and Helobiales, may have originated independently from similar protangiospermous ancestors. Hutchinson, one of the most recent advocates of the monophyletic origin of the monocotyledons, separates from the Ranales the Magnoliaceae and related families as a distinct order Magnoliales. These are predominantly trees and shrubs, while the other Ranales are mostly herbaceous types, and from the latter it is assumed the monocotyledons have been derived.

The Centrospermae may be regarded as the lowest order of the Dialypetalae, related to the apetalous Polygonales and possibly to the Piperales. In some of them, e.g., Amaranthus and Chenopodium, the perianth is composed of inconspicuous foliose segments and sometimes the flowers are diclinous. In other centrospermous types, e.g., Abronia and Mirabilis, the flowers are monochlamydeous but the calyx is petaloid and resembles a sympetalous corolla. The showy petaloid perianth in these forms is evidently a modification of foliose organs (sepals) and is not homologous with true petals, which are equivalent to stamens (sporangiophores). The apetalous forms, with a single basal ovule, recall the Piperales, which they further resemble in the development of perisperm in the seed.

In the more primitive Ranales, like *Anemone* and *Caltha*, the numerous carpels are free, and the stamens and perianth segments are variable in number. The perianth is not differentiated into calvx and corolla.

In the more specialized Dialypetalae there is a very definite calyx and corolla. The sepals are often more or less completely united into a tubular or cup-shaped calyx, but the petals are always free. In the more advanced forms the parts of the flower are definite in number, with sepals and petals most commonly 4 or 5, the stamens the same or double, and the carpels most commonly less in number and united into a compound pistil. The less specialized flowers are radially symmetrical (actinomorphic), e.g., Rosa, Oxalis, and Ranunculus; but there are numerous zygomorphic types, e.g., Delphinium, Viola, Papilionaceae, and Pelargonium. The flower may be hypogynous (ovary superior), perigynous (partial cohesion of ovary and floral axis), or epigynous (ovary "inferior"—completely coalescent with the floral axis). Among the Dialypetalae are very many specialized structures of both the vegetative and the reproductive organs.

CLASSIFICATION OF CHORIPETALAE

There is no general agreement as to the number and scope of the orders of the Dialypetalae. Engler recognizes 13 and Wettstein 15; but Hutchinson, who believes all of the dicotyledons may be traced back to two orders, Magnoliales and Ranales, proposes 59 orders of Archichlamydeae including both Apetalae and Dialypetalae.

The following list, based mainly on Engler and Wettstein, will be employed in the discussion of the Choripetalae: (1) Centrospermae; (2) Ranales; (3) Hamamelidales; (4) Euphorbiales; (5) Rhoeadales; (6) Sarraceniales; (7) Rosales; (8) Geraniales; (9) Sapindales; (10) Rhamnales; (11) Malvales; (12) Parietales; (13) Guttiferales; (14) Opuntiales; (15) Myrtales; (16) Umbelliflorae.

The Centrospermae and the Ranales are generally recognized as the most primitive orders. The Euphorbiales (Tricoccae) seem also to be a very primitive group not clearly related to any other order, and probably should be recognized as a distinct order. The same may be said of the Hamamelidales. These two orders are perhaps to be placed between the Apetalae and Dialypetalae.

ORDER 1. CENTROSPERMAE

The simplest of the Centrospermae—the Amarantaceae and Chenopodiaceae have flowers with inconspicuous perianths, and sometimes diclinous. The Phytolaccaceae—e.g., Phytolacca, "pokeweed," and the Nyctaginaceae, e.g., Miriabilis and Abronia—are apetalous; but the perianth is petaloid and resembles a sympetalous corolla. The Aizoaceae, represented by the showy-flowered species of Mesembryanthemum, sometimes have petals, or may be apetalous. In Mesembryanthemum there are many stamens and the "petals" are really staminodia. In the Portulacaceae, e.g., Portulaca, Calandrinia, and Claytonia, the perianth is differentiated into

a calyx of two sepals and a corolla with five petals, and there are five stamens.

In the most specialized family, the Caryophyllaceae, the sepals may be united into a tubular calyx, e.g., *Dianthus* and *Silene*, and the petals are very conspicuous. In the lower members of the order, e.g., *Chenopodium*, the ovary contains a single basal ovule, much as in the Polygonales or the Piperales. In the more advanced forms there are several carpels united into a syncarpous ovary, either unilocular (Caryophyllaceae) or

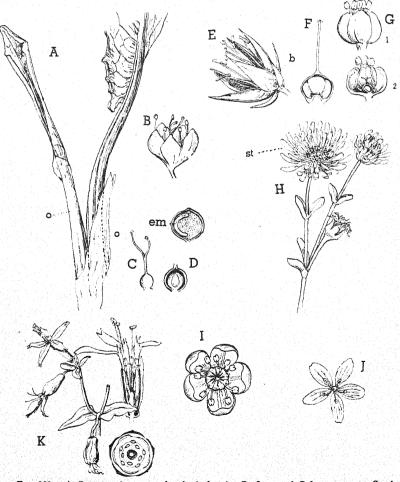


Fig. 329.—A, Rumex crispus; o, sheath (ochrea); B, flower of Polygonum sp.; C, pistil of Polygonum; D, ovary and seed; em, embryo; E, F, Celosia cristata; G, Chenopodium album; H, Mesembryanthemum sp.; st, staminodia; I, Phytolacca decandra; I, Claytonia virginica; K, Silene virginica.

plurilocular (Phytolaccaceae). In the latter each loculus contains a single basal ovule. In the Caryophyllaceae there is a central placenta bearing numerous ovules.

ORDER 2. RANALES (POLYCARPICAE)

The Ranales are of especial interest since they are often regarded as the most primitive of the angiosperms, from which not only the more specialized dicotyledons but the monocotyledons as well have been derived. However, this assumption of a monophyletic origin of the angiosperms does not seem to be warranted from a study of ontogeny and the geological record.

The order is a large one and perhaps should be separated into at least two—the Ranales in which a large majority are herbaceous plants; and

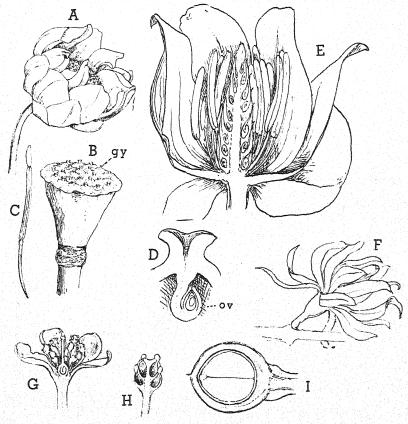


Fig. 330.—A, Nelumbo lutea; B, enlarged receptacle of Nelumbo, bearing the carpels, gy; C, stamen; D, apex of carpel, showing the ovule; E, Liriodendron tulipifera; F, Calycanthus floridus; G, H, Umbellularia californica; H, stamen of Umbellularia; I, section of ripe fruit of Umbellularia.

the Magnoliales, composed almost exclusively of trees and shrubs. Some of the former are aquatics, and recall the monocotyledonous Helobiales, with which they may be remotely related. Some of the Ranales show distinctly monocotyledonous characters in the stem structure, which in section shows a distribution of the vascular bundles like that of the monocotyledons. Examples of such stems are found in *Podophyllum*, *Thalictrium*, *Nymphaea*, and *Anemone Japonica*. The floral structures also suggest the monocotyledons.

The flowers are typically apocarpous. There may be a single carpel, e.g., Berberidaceae, Lauraceae, and *Ceratophyllum*. In some of the Nymphaeaceae the carpels are completely united into a compound ovary.

Classification.—The two most primitive families of the Ranales—Ceratophyllaceae and Nymphaeaceae—are aquatics. The first includes some three species of Ceratophyllum, submerged aquatics, with leaves divided into slender divisions. The monoecious flowers with inconspicuous perianth have either a number of stamens or a single carpel. The genus is cosmopolitan.

The Nymphaeaceae include the showy water lilies (Nymphaea, Nuphar, and Nelumbo) and the inconspicuous water shields, Brasenia and Cabomba. The former is cosmopolitan; the latter occurs in tropical America. The flowers in the latter genera are of the monocotyledonous type—viz., perianth of six similar members; stamens 3–18; carpels indefinite. The showy lotus (Nelumbo) has many separate carpels sunk in cavities in the conspicuous, top-shaped receptacle. There are but two species of Nelumbo: N. lutea, of the Eastern States; and N. nucifera, the Oriental lotus of eastern Asia. Nymphaea (Castalia) has a good many species throughout the temperate and tropical zones. Nuphar, the yellow water lily, is restricted to the North Temperate Zone. The famous Victoria regia of the Amazon, as well as some other tropical genera, belong to the Nymphaeaceae.

In Nuphar there is a suggestion of the arrow-shaped leaves of Sagittaria. The seedling of some of the water lilies also has the early leaves sagittate, like the monocotyledonous Sagittaria.

The relationships of the Nymphaeaceae have been the subject of some controversy, and they have even been placed among the monocotyledons. Not only are there similarities in the tissues, and floral structures, especially of the simpler forms like *Brasenia* and *Cabomba*, but the embryos of *Nymphaea* and *Nelumbo* according to Cook and Lyon are intermediate in character between monocotyledons and dicotyledons, the two cotyledons arising by the division of a common primordium.

The great majority of the large family Ranunculaceae are restricted to the North Temperate Zone and are almost wanting in the tropics. A small number of species belonging to the simpler genera, e.g., Anemone, Ranunculus, and Clematis. Caltha and Myosurus are found also in the South Temperate regions of South America and Australasia. With very few exceptions the Ranunculaceae are herbaceous, mostly perennial plants. The most marked exception is Clematis, with many woody species. In some other genera, e.g., Thalictrum, the sepals are usually inconspicuous and may be deciduous. The stamens, however, are conspicuous. In some species of Thalictrum and Clematis the flowers are dioecious. Within the family there are all gradations from such presumably primitive types to highly specialized dialypetalous genera like Aquilegia, Delphinium, and Aconitum. These are all dialypetalous, but both calyx and corolla are similarly colored. In Delphinium and Aconitum the flowers are strongly zygomorphic.

In the less specialized genera like Ranunculus and Anemone the carpels and stamens are indefinite in number and the fruit is a one-seeded fruit, an "achene"; but in the more specialized genera, the number of carpels and stamens is reduced occasionally to a single one, and the fruit is a pod or "follicle," containing several seeds.

The carpels are sometimes borne on an elongated receptacle, which is especially conspicuous in some species of *Ranunculus* and *Anemone* and still more so in *Myosurus*. In the latter the pistillate receptacle recalls the

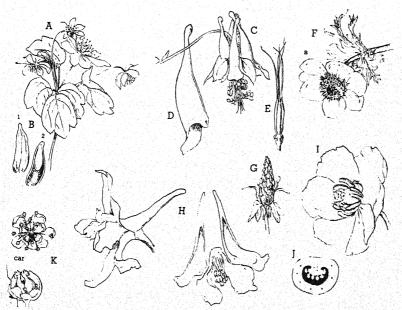


Fig. 331.—A, B, Syndesmon thalictroides; C-E, Aquilegia canadensis; F, Anemone coronaria; G, Myosurus minimus; H, Delphinium tricorne; I, J, Podophyllum peltatum; K, Menispermum canadense (G, after Britton and Brown).

spike of some of the Piperales, and the resemblance between the flowering spike of Anemopsis, a member of the Sauraceae, and the pistillate receptacle of Myosurus or Anemone is evident. This resemblance is increased by the petal-like bracts at the base of the inflorescence in Anemopsis. This resemblance might be cited in favor of Wettstein's theory that the angiospermous flower is to be interpreted as derived from an inflorescence composed of unisporangiate flowers.

Related to the Ranunculaceae but differing in some important respects is the family Berberidaceae. The species of Berberis, the type genus, are shrubs of moderate size; but all the other genera except one, Nandina, are herbaceous. The parts of the flowers are for the most part in three's, but there is only a single carpel. Berberis is a large genus with species distributed throughout temperate Eurasia and North America. The other genera with very few species are, except Nandina, all herbaceous and are mostly confined to eastern Asia and Atlantic North America. Among these are Podophyllum, Jeffersonia, and Diphylleia. Somewhat more widespread are Caulophyllum and Epimedium. These isolated genera are probably relicts of a once extensive Tertiary flora.

In contrast to these four families are about a dozen families of trees and shrubs with flowers of the ranalean type. These perhaps had best be placed in a separate order.

MAGNOLIALES

The Magnoliales are represented in the United States by several families, viz., Magnoliaceae, Calycanthaceae, Anonaceae, Menispermaceae, and Lauraceae; but these include only a small number of species, the great majority being tropical. The simplest form of flower is represented by the Lauraceae, e.g., Umbellularia. The perianth is composed of two whorls of three similar segments, and the nine stamens are in three series. The single carpel has a solitary ovule. The flower is much like that of the Berberidaceae. In Sassafras, also of the Lauraceae, the flowers are dioecious, the staminate flower having nine stamens and the pistillate six rudimentary ones. The flower is thus suggestive of the simple monocotyledonous floral type.

In the Magnoliaceae the floral structure is more like that of the Nymphaeaceae, where there is a multiplication of all the floral organs. Between the extremes shown by *Magnolia* and the Lauraceae are numerous intermediate forms.

The Magnoliaceae are represented in eastern United States by several species of Magnolia, of which M. grandiflora is the most familiar. The other species of the genus belong to eastern Asia. In the same family is the tulip tree, Liridendron tulipifera, the only species except for a very

similar one in China. The tulip tree or "poplar," as it is often incorrectly called, is one of the largest and most important timber trees of eastern United States. A third genus, Illicium, with inconspicuous flowers, has two species in the Gulf States. The others are from eastern Asia.

Most of the Magnoliaceae belong to the Northern Hemisphere; but one genus, Drimys, is predominantly Austral. The South American species, D. Winteri, occurs also in Mexico; but most of the species are found in New Zealand and Australia. A peculiarity of Drimys is the structure of the wood, which is composed of pitted tracheids with no vessels and thus resembles the typical coniferous wood.

Two families, Anonaceae and Myristicaceae, with few exceptions are tropical trees or shrubs. Several species of Anona, including the custard apple and cherimoya, are cultivated in Florida and southern California. One genus, Asimina, is native in eastern United States. A. triloba is the

pawpaw of the Middle West.

The nutmeg family, Myristicaceae, contains but a single genus, native to the East Indies. M. fragrans is the cultivated nutmeg. The flowers are dioecious, with the stamens united by the coherent filaments. There is a

single carpel with a solitary ovule.

The Lauraceae, the largest family of the order, is cosmopolitan and includes several hundred species-mostly tropical or subtropical. Two regions are especially rich in Lauraceae, the East Indies and Brazil. In the United States are several species of Lindera, Litsia, Persea, and Sassafras. The only representative on the Pacific Coast is the beautiful bay tree, Umbellularia californica, much resembling the classical bay (Laurus nobilis) of southern Europe. Persea gratissima is the familiar "avocado" or alligator pear, now cultivated extensively in Florida and in southern California. Sassafras, with a single species, S. officinale, is found only in eastern United States and Canada.

The most aberrant genus of the Lauraceae is Cassytha, including leafless parasites with the habit of dodder (Cuscuta)-twining about other stems and sending haustoria into the tissues of the host. One species, C. filiformis, is widespread in the tropics.

That the Lauraceae are very old types is indicated by fossil remains in the Cretaceous and Early Tertiary. Among these, in the Lower Cretaceous (Patapsco) formation, species of Sassafras have been reported.

Two other orders are represented in the United States—Calycanthaceae and Menispermaceae. The former has only four species, which may be included in the genus Calycanthus; of these C. Florida, "sweet-scented shrub," and C. fertilis are native in the southern Atlantic States, C. occidentalis is on the Pacific Coast, and C. praecox (Chimonanthus fragrans) from Japan is in cultivation.

The flowers have numerous sepals, petals, and stamens, and free carpels, which with the stamens are included in an urn-shaped receptacle.

The large, mainly tropical family Menispermaceae has only a few representatives in temperate regions. Three genera—Menispermum, Cocculus, and Calycocarpum—each with a single species are found in the United States. They are woody climbers, like most of the members of the order. The flowers are dioecious—the staminate flowers with numerous (12–24) stamens and the pistillate with several (3–6) carpels.

The geological record shows that the Magnoliales were represented in the Cretaceous by members of several families—Magnoliaceae, Lauraceae, and Menispermaceae—indicating the great antiquity of the order.

ORDER 3. HAMAMELIDALES

The two families included by Wettstein in the Hamamelidales, viz., Hamamelidaceae and Platanaceae, are more commonly associated with Saxifragaceae; but there are reasons for placing them in a special order, perhaps intermediate between the Apetalae and the Choripetalae. Some of them have monoecious, apetalous flowers, and they are found as fossils in the Cretaceous rocks. Of the three genera represented in the United States—Hamamelis, Liquidambar, and Platanus—the first two are confined to the Eastern States, while the sycamore, Platanus, has one species in the Eastern States and one in California. Besides Hamamelis virginica, the witch hazel, there are two other species in Japan and China.

The flowers of *Hamamelis* are hermaphrodite and have both calyx and corolla. In *Liquidambar* and *Platanus* they are apetalous, recalling the flowers of some of the Moraceae.

ORDER 4. EUPHORBIALES (TRICOCCAE)

The systematic position of the Euphorbiaceae is difficult to determine. They differ greatly from any other family, and probably are best considered as a separate order. Wettstein apparently regards the order as a primitive one, but Engler places them next to the Gruinales, a somewhat specialized order of Dialypetalae.

The great number and variety of genera and species in the family would rather indicate a more recent and more specialized group. The family Euphorbiaceae, the only one in the order, is a very large one, with over 200 genera, of which the largest, Euphorbia, is cosmopolitan and has more than 600 species. The Euphorbiaceae range from small annual herbaceous weeds, through every degree of herbaceous and shrubby species, to trees of large size. They are highly developed in the warmer regions, and especially in the tropics. Most genera are limited in their range, but a few, like Euphorbia, Phyllanthus, and Croton, have a wide distribution. In the hot dry regions of Asia and Africa some of the Euphorbias simulate the

American spiny cacti and are sometimes mistaken for them, but can be at once distinguished by their milky latex.

The flowers are inconspicuous for the most part, but in some of the Euphorbias the inflorescence is surrounded by showy bracts. Thus in E. corollata and E. fulgens the insignificant flowers are enclosed in a cupshaped involucre with petal-like marginal bracts, so that the inflorescence exactly resembles a five-petaled flower. In the familiar poinsettia (E. pulcherrima) the large scarlet bracts surround a group of involucres. Many Euphorbiaceae are of great economic importance—Manihot utilissima furnishes cassava, the most important food plant of Brazil, and also tapioca. The milky latex of some species is the source of rubber, the most important being "Para" rubber, the product of the Brazilian Hevea brasiliensis, now extensively grown in many tropical countries. The familiar castor bean, Ricinus communis, also belongs to the Euphorbiaceae.

The Euphorbiaceae resemble the lower Monochlamydeae in the simple structure of their flowers. These are diclinous, and may be greatly reduced in structure. In *Euphorbia* the flower has no perianth and consists of a single stamen or pistil—the latter composed of three united carpels, each loculus containing a single ovule. The pistil is borne on an elongated stalk.

ORDER 5. RHOEADALES

Like the Ranales, the Rhoeadales are for the most part restricted to the North Temperate Zone, although there are some which are tropical or South Temperate. The most important families are the Papaveraceae, the Cruciferae, and the Capparidaceae.

PAPAVERACEAE

The poppy family, Papaveraceae, includes a number of genera with showy flowers. Papaver is best developed in Europe and temperate Asia. Peculiarly American are Sanguinaria, of eastern United States, and several genera in the Western States, e.g., Argemone; Eschscholtzia, the California poppy; Romneya; and several others. The flowers are hypogynous, with the carpels united into a compound pistil. The perianth most commonly has two sepals, which are shed when the flower opens. In Eschscholtzia they are united into a cap. The petals are most commonly 4; but in Sanguinaria, there may be 8–12. The stamens are numerous and the carpels two to many, united into a compound pistil. In the Fumarioideae, often separated as a distinct family, there are always 6 stamens and the flowers are strongly zygomorphic, the petals being saccate. The most familiar example is the garden "bleeding heart," Dicentra spectabilis.

Many of the Papaveraceae have milk tubes, containing latex—white in Papaver, yellow in Argemone, red in Sanguinaria.

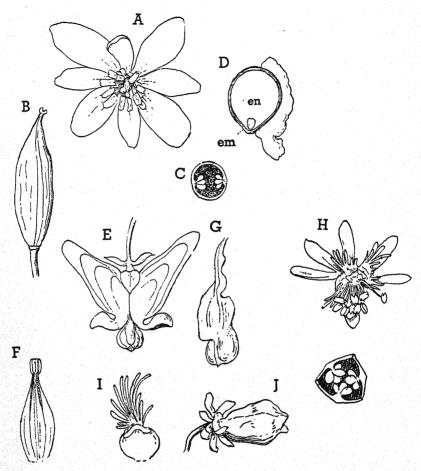


Fig. 332.—A-D, Sanguinaria canadensis; E-G, Dicentra cucullaria; F, stamens; G, a single petal; H-J, Reseda odorata.

CRUCIFERAE

The mustard family, Cruciferae, is a very large and natural one, including over two hundred genera. The Cruciferae are quite cosmopolitan, although best developed in the North Temperate Zone. Their floral structure is extraordinarily uniform. There are 4 deciduous sepals, 4 conspicuous petals, 6 stamens in two sets ("diadelphous"), and 2 (sometimes 4) carpels. They are mostly annual or biennial herbs, and rarely develop permanent woody stems. The character of the fruit is important in their classification. The fruit is a pod (silique, silicle), usually divided by a thin median partition into two valves. Sometimes the pod is indehiscent and breaks transversely into several joints.

CAPPARIDACEAE

The Capparidaceae are for the most part tropical and subtropical and include both herbaceous and shrubby species. The type genus, Capparis, contains about one hundred fifty species in the warmer regions of both hemispheres but is absent from North America. There are a few representatives of the family in the United States, mostly in the Southwest. The commonest genus is Cleome, "spiderflowers," common in the Western States from the plains to the Pacific Coast.

The mignonette, Reseda odorata, represents the family Resedaceae.

ORDER 6. SARRACENTALES

Among the most remarkable of the dicotyledons are the three families, Sarraceniaceae, Nepenthaceae, and Droseraceae, which have been associated in the order Sarraceniales. It is doubtful, however, if they are really related, and their inclusion in a single order is perhaps based on physiological rather than on morphological characters. They are the most notable of the "insectivorous" plants, and have developed highly specialized leaf structures which serve as traps; sometimes, at least, there is a true digestion of the captured prey.

The Sarraceniaceae include the pitcher plants of North America; the Nepenthaceae, the pitcher plants of tropical Asia; while the Droseraceae are cosmopolitan.

SARRACENIACEAE

Sarracenia purpurea, the common pitcher plant, represents the family in northern United States and Canada, while there are about half a dozen other species in the southeastern states. In northern California and Oregon the related Darlingtonia californica replaces Sarracenia. In both genera the leaves are trumpet-shaped, with a lid-like expansion above the orifice. In Darlingtonia the upper part of the leaf is bent over, forming a hood with an opening at the base. The inner wall of the pitcher has glands on it which secrete a fluid having some digestive effect upon the insects which have been trapped. The large solitary flowers resemble those of the Nymphaeaceae, e.g., Nuphar, and in connection with the subaquatic habit of most species support the view that the Nymphaeaceae are probably the nearest relatives of the family. Except for the monotypic Heliamphora nutans from Guiana, the Sarraceniaceae are restricted to North America.

NEPENTHACEAE

The Nepenthaceae, with about forty species of Nepenthes, are especially abundant in the Malay Peninsula and Borneo, the latter having about half of the known species. A few occur in other parts of the Malay Archipelago and in northern Australia, and extend to Madagascar and the Seychelles in the Indian Ocean. In Borneo they are extremely common and

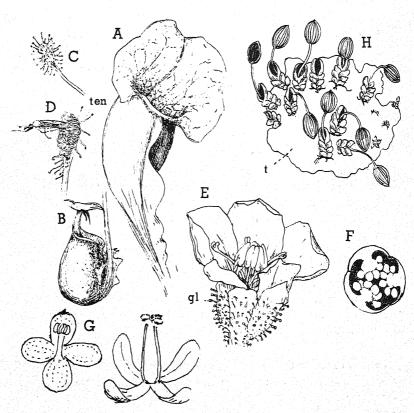


Fig. 333.—A, leaf of Sarracenia purpurea; B, leaf of Nepenthes sp.; C-F, Drosera intermedia; G, flowers of Nepenthes; H, Podostemon olivaceum (B, after Goebel; G, after Engler and Prantl; H, after Warming).

reach their maximum development, the pitchers in some species, e.g., N. rajah, being a foot or more in length. Some of the smaller forms have the leaves in close rosettes in the ground, and the whole leaf forms the pitcher, as in Sarracenia. Most of them, however, are climbing or epiphytic in habit. The apex of the leaf develops into a tendril at the tip of which the pitcher is formed.

The flowers in Nepenthes are very different from those of Sarracenia. The dioecious flowers form an elongated, terminal inflorescence. The perianth consists of 4 sepals, and the staminate flower has the stamens united into a central column. The pistillate flower has 4 almost separate carpels. The floral structures might be compared with those of some of the simpler Ranales. It is very doubtful if there is any real relationship with the Sarraceniaceae, and in any case it must be remote.

DROSERACEAE

With the exception of about half a dozen species, of extremely restricted range, all of the Droseraceae belong to the genus *Drosera*. They probably number about one hundred species, which are found from Patagonia and the Auckland Islands south of New Zealand to the arctic timber line of Europe, Siberia, Canada, and Alaska.

The "sundews" are familiar bog plants, the common species having the spatulate leaves with numerous sticky tentacles and glands which are effective traps for the capture of small insects. The flowers differ much from those of the other two families and are much more like those of some of the Saxifragaceae. In *Drosera* there are a cup-shaped calyx, 5 showy petals, 5, or sometimes more, stamens, and 3–5 carpels. The ovary is unilocular, with parietal placentae. The genus reaches its maximum development in the temperate regions of South Africa and especially in western Australia, where probably at least half of the known species are found.

There are five other genera—three monotypic, the others each with two species—all of them greatly restricted in their range. The best-known of these is the "Venus' flytrap," Dionaea muscipula, restricted to the coastal region of the Carolinas.

ORDER 7. ROSALES

The order Rosales is one of the largest among the angiosperms, and includes many common flowers of the North Temperate Zone. In the lower types, e.g., Crassulaceae and many Rosaceae, all of the floral organs are separate, thus recalling the Ranales, with which they are probably distantly related. The perianth is differentiated into calyx and corolla, sepals and petals, being in most cases five in number. The stamens may be numerous, or the same number as the petals. In many cases, e.g., Rosaceae, the sepals are united, and the stamens are inserted on the margin of the cup-shaped calyx. The carpels may be separate, e.g., Rosa and Crassulaceae, or they may be united. The flower may be hypogenous or there may be an inferior ovary. The two most important families are the Rosaceae and the Leguminosae. Each of these has three subfamilies, often treated as independent families.

ROSACEAE

The Rosaceae are predominantly northern in their distribution, with few representatives in the tropics and Southern Hemisphere.

On the basis of the carpellary structure, the family is divided into three sections, often considered distinct families, viz., Rosaceae, Pomaceae, and Drupaceae. In the Rosaceae proper there are numerous separate carpels, very much as in the Ranunculaceae. These may be inserted separately on a receptacle, and the fruit is an achene or nutlet like that of Ranunculus, e.g., strawberry. In Rosa the crowded pistils are included in the hollow receptacle, which later becomes fleshy but does not completely invest the fruits developed from the individual pistils. In the Pomaceae the carpels are completely coherent with the greatly enlarged calyx, which forms the juicy "fruit" of the apple or pear. In the Drupaceae there is a single carpel, which contains a single ovule. The calyx is shed and the juicy pulp of the fruit is formed from the wall of the ovary which closely invests the seed. The inner tissue (endocarp) forms the "stone," the seed being the kernel, e.g., in cherry, plum, and peach. The embryo in most Rosaceae completely fills the embryo sac, i.e., the seeds are exalbuminous; but there are some exceptions where the embryo is embedded in endosperm, as it is in the Ranunculaceae.

SAXIFRAGACEAE

Some other characteristic families of the Rosales are the Podostemaceae, the Saxifragaceae, the Cephalotaceae, and the Pittosporaceae. The largest of these families, the Saxifragaceae, like the Rosaceae, has most of its species restricted to the North Temperate regions. There are both herbaceous and woody types. Among the former are the many species

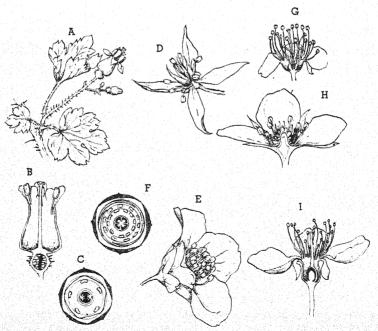


Fig. 334.—A-C, Ribes Cynosbati; D, Sedum sp.; E, F, Philadelphus grandiflorus; G, Spiraea sp.; H, Fragaria virginica; I, Prunus cerasus.

of Saxifraga; also in the north woods and bogs are species of Mitella, Parnassia, Tiarella, Heuchera, and others. There are some showy shrubs, like Hydrangea, Philadelphus, and Escallonia. The latter with several species from temperate South America is often seen in Californian gardens.

CEPHALOTACEAE

The Cephalotaceae are represented by the monotypic Cephalotus follicularis, a curious pitcher plant, with pitchers much like those of Nepenthes. It is known from only a very limited region in western Australia, and the family is sometimes united with the Saxifragaceae. Also usually associated with the Saxifragaceae are the currants and gooseberries (Ribes), sometimes separated as a family, Grossulariaceae.

PITTOSPORACEAE

Pittosporum, with about seventy species, includes a majority of these species, which are found in the tropical and subtropical regions of the Old World, including Polynesia. Several species from Australia, New Zealand, and Japan are handsome evergreen shrubs, with sweet-scented flowers, and are often cultivated in California. The flowers have five sepals, petals, and stamens, all free, and 2–5 carpels, and resemble the simpler Saxifragaceae. The greater number of species are found in Australia, New Zealand, and Hawaii. In addition to Pittosporum are eight other genera, all confined to Australia.

The relationships of the Pittosporaceae are not entirely clear, but they may perhaps best be placed near the Saxifragaceae.

PODOSTEMACEAE

Among the most remarkable of the dicotyledons are the Podostemaceae. They are mostly tropical aquatic forms growing in rapid streams, under waterfalls, and attached by special holdfasts to rocks and stones, recalling many marine algae, some of which they resemble also in form. The plant body in the Podostemaceae is profoundly altered and is principally made up of roots, which may be flattened and provided with chlorophyll, so that they form a broad thallus from which the flowering shoots arise.

Willis has made an extensive study of a number of Indian and Ceylonese species. He agrees with Warming that the "thallus" is a modified root, which may be filiform, cylindrical, or flattened, and in quiet water may be free except for a basal holdfast. The primary shoot has a very limited growth and very early develops a root at the base, which forms the thallus. The secondary shoots, which bear the flowers, are developed endogenously from the thallus, like secondary roots.

The flowers are inconspicuous, in a few cases having several free sepals but more often having no perianth. There are one to many stamens and most commonly there are two carpels. The relationships of the Podostemaceae are very obscure. Warming thinks they are nearest the Saxifragaceae; Willis suggests the possibility of their origin from some ancient water plants allied to the Nymphaeaceae.

LEGUMINOSAE

The cosmopolitan family, Leguminosae, is the largest of the Dialypetalae, and has many species in all parts of the world. In most of the North Temperate Zone, including the United States, the majority of species are herbaceous; but there are some shrubs and trees and some woody vines. The locust (Robinia), the honey locust (Gleditschia), and the Judas tree (Cercis), as well as some others, are trees of good size; and in Europe various species of broom, Genista and Cytisus, are shrubs. In the warmer regions, especially the tropics, are many showy trees, shrubs, and woody climbers or lianas.

The leaves of the Leguminosae are commonly pinnately compound, but ternately divided leaves like clover or beans are common. Simple leaves are rare. The Leguminosae always have associated with their roots a nitrogen-fixing bacterium (Bacillus radicicola), which causes characteristic tubercles on the roots.

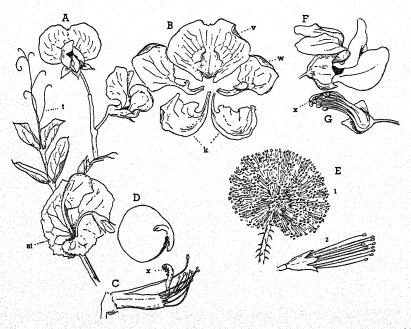


Fig. 335.—A-D, Pisum sativum; C, diadelphious stamens, and pistil, x; E, Schrankia uncinata; E, 2, single flower; F, G, Cercis canadensis.

The essential floral structure is similar in all of them; but there are many modifications, so that the family has been divided into three well marked subfamilies, perhaps better regarded as families. These are the Mimosaceae, the Caesalpiniaceae, and the Papilionaceae (Fagaceae).

The simplest floral type is that of the Mimosaceae. The flowers are sometimes diclinous but are typically hermaphrodite. The perianth is inconspicuous but as a rule has both calyx and corolla; the former is sometimes obsolete but usually forms a cup-shaped calyx. When the calyx is wanting, the petals may be united into a sympetalous corolla. The stamens may be 5–10, but in *Acacia* they are numerous. In the Mimosaceae it is the stamens which form the showy part of the flower. The pistil, as in all the Leguminosae, is a single carpel, which develops with the characteristic "legume," or pod. The structure of the flower in the Mimosaceae is actinomorphic and may be compared with that of the lower Rosaceae, especially the Drupaceae.

In the Caesalpiniaceae, the flowers are often extremely showy and the petals large and brilliantly colored. The stamens most commonly are ten. Some of the lower types, e.g., Gleditschia, have almost actinomorphic flowers, but in most of them there is marked zygomorphy. In Cercis there is a close approach to the floral type of the Papilionaceae, the predominant family in the temperate zones. In the Papilionaceae the flower is strongly zygomorphic. The upper petal forms the "standard," the two lateral ones form the "wings," and the two lower ones, united by their outer edges, form the "keel," within which are the ten stamens and the pistil. The fruit of the Leguminosae is a pod, usually opening by two valves but sometimes indehiscent and in some cases breaking up into segments. In the Papilionaceae the ripe seeds have little or no endosperm, and the embryo completely fills the seed. In the Mimosaceae and the Caesalpiniaceae the embryo is less developed and there may be a much larger amount of endosperm in the seed.

Mimosaceae.—The Mimosaceae are mostly trees and shrubs; but there are a few herbaceous types, like the "sensitive plant," Mimosa pudica. The largest genus is Acacia, with species throughout the tropical and subtropical zones but especially abundant in the more arid districts. The genus reaches its greatest development in Australia, whence many species have been introduced into the Mediterranean countries and into California. Species of Mimosa and Albizzia also are cultivated.

Caesalpiniaceae.—The Caesalpiniaceae, like the Mimosaceae, are confined to the warmer parts of the world. In the United States the honey locust (Gleditschia triacanthos) and the redbud (Cercis) are the best-known examples. In the Southern States are several species of Cassia, herbaceous plants with yellow flowers. In the tropics Cassia is represented

by nearly four hundred species, including some very showy ones, e.g., the "golden shower" (C. fistula), which are favorite ornamental trees in Hawaii and other tropical countries. The family includes many other ornamental trees and vines, e.g., Poinciana regia, Amherstia nobilis, and species of Bauhinia. The flowers in the Caesalpiniaceae are open, the petals generally spreading but more or less markedly zygomorphic.

Papilionaceae.—In the Papilionaceae the familiar pea-shaped flower is almost universal. The stamens are "diadelphous"; i.e., nine are united into

a tube, and the tenth is free.

There are some three hundred genera, with over seventy thousand species. Some genera, e.g., *Trifolium*, *Lupinus*, *Phaseolus*, and *Vicia*, have a hundred or more species, while *Astragalus* has over a thousand. The Papilionaceae include many of the most important food plants for both domestic animals and man.

While the three families of the Leguminosae are well-defined, there are nevertheless genera which are more or less intermediate in character and show the evident relationships between them. The Mimosaceae and the Caesalpiniaceae may be assumed to be older types than the Papilionaceae, as their flowers approach more the type of the simpler Rosaceae, with which the Leguminosae seem to be most nearly related. That the Mimosaceae and the Caesalpiniaceae are old types is indicated, although the data are incomplete. It is certain that some of the living genera existed in Early Tertiary time and probably in the Upper Cretaceous, where a species of Bauhinia has been reported. Cercis is definitely known from the Oligocene, and Gleditschia is also reported from the Early Tertiary.

ORDER 8. GERANIALES

The Geraniales include about twenty families, among which are Geraniaceae, Oxalidaceae, and Tropaeolaceae (the two latter sometimes are united with the Geraniaceae), Rutaceae, Malpighiaceae, Simarubaceae, and several others. They may be herbaceous, like most of the species of Geranium, Oxalis, and most of the species of the colder regions. A much larger number are trees or shrubs, inhabiting the tropical and subtropical countries.

The flowers are usually actinomorphic and pentamerous. The stamens 5–10, carpels 5. In *Pelargonium* the flower is conspicuously zygomorphic and some of the stamens are abortive. In *Tropoeolum*, the flower is also zygomorphic and there are only three carpels. The showy garden "geraniums" are varieties of *Pelargonium* from South Africa. The wild species of *Geranium* are common in the North Temperate Zone. One of the commonest weeds in California, *Erodium cicutarium*, was introduced presumably from southern Europe. Two families of the Geraniales are of great economic importance—the flax family, Linaceae, and the Rutaceae, to

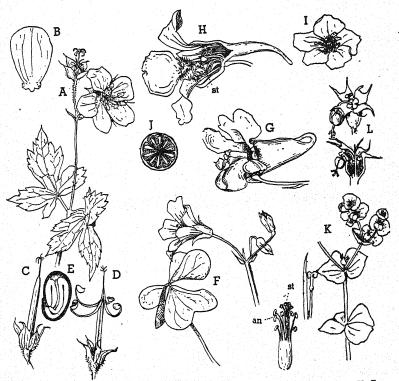


Fig. 336.—A-E, Geranium maculatum; F, Oxalis violacea; G, Impatiens fulva; H, Tropoeolum; majus; st, stamens; I, J, Linum virginianum; K, L, Euphorbia commutata.

which the citrus fruits belong. In the warmer parts of the United States one often sees the "umbrella tree," or "Chinaberry," *Melia Azederach*, an Indian tree which represents the Meliaceae, a large family of tropical trees, e.g., mahogany (*Swietenia*) and Spanish cedar (*Cedrela*).

The conspicuous yellow flowers of Malpighia are a feature of the American tropics, where the Malpighiaceae reach their greatest development. Some of these are woody climbers, "lianas."

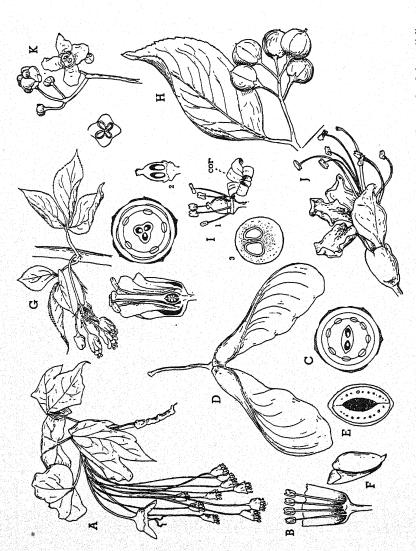
The Simarubaceae are mostly restricted to the tropics, but one tree, Ailanthus glandulosa, "tree of heaven," introduced from China, is often planted as a shade tree.

ORDER 9. SAPINDALES

Most of the Sapindales are trees or shrubs, but two families, Limnanthaceae and Balsaminaceae are herbaceous. While the majority are tropical or subtropical, there are a number of characteristic northern types, e.g., maples (Aceraceae) and buckeyes (Hippocastanaceae). There are about

twenty families, of which the following may be mentioned: Buxaceae, Limnanthaceae, Anacardiaceae, Aquifoliaceae, Celastraceae, Aceraceae, Hippocastanaceae, and Balsaminaceae.

The flowers are mostly 4–5 parted, with 4–5 stamens and 2–5 carpels. Sometimes they are diclinous. The Buxaceae, a small family, have apetalous flowers; but in the others calyx and corolla are present, the calyx being usually cup-shaped. The Limnanthaceae is a small family with only two



Staphylea trifolia; as flower opens; J, flower of Aesculus glabra; K, Fig. 337,--A-C, Acer saccharum; D-F, A. saccharinum; F, embryo removed from the seed; H, Celastrus scandens; I, Vitis labrusca; cor, corolla, thrown Euonymus atropurpureus.

100

genera, exclusively American. Limnanthes douglasii is a pretty spring flower in California. The Anacardiaceae, a large family, mainly tropical, includes several species of Rhus, among them several poisonous species—"poison oak," "poison ivy," etc. There are also a number of important fruits, especially the mango (Mangifera indica). The pepper tree (Schinus molle) is also a member of the Anacardiaceae. The species of holly (Ilex) represents the small family Aquifoliaceae, and species of Evonymus and Celastrus are examples of the Celastraceae. Celastrus scandens is the "bittersweet" of eastern United States.

The Aceraceae, essentially northern types, are represented by a number of species of Acer throughout the North Temperate Zone. Acer saccharum is the sugar maple of the northeastern states. Aesculus includes the American "buckeyes" and the European horse chestnut, which compose the family Hippocastanaceae. The flowers are notably zygomorphic. This is also the case in the Balsaminaceae, a family with some two hundred fifty species, all but two belonging to the genus Impatiens; they are delicate herbaceous plants, with showy zygomorphic flowers. The garden balsam, I. balsamina, and several other species are common in cultivation. Most of the species are tropical, but in the Eastern States are two wild ones, I. pallida and I. biflora.

ORDER 10. RHAMNALES

The Rhamnales include two families, Rhamnaceae and Vitaceae. They are all trees or shrubs or woody climbers, with stem tendrils. The majority are tropical, but there are some representatives in the temperate zones. Rhamnus has several species in Eurasia and temperate America. Also belonging to the Rhamnaceae are the numerous species of Ceanothus, "wild lilac" of the Pacific Coast. The Vitaceae include about a dozen species of grapes (Vitis) in the United States, and species of Cissus and Ampelopsis. The European wine grape, Vitis vinifera, is extensively cultivated in California.

ORDER 11. MALVALES (COLUMNIFERAE)

The Malvales may be herbaceous, trees, or shrubs. Many of them have large and showy flowers. The stamens are in most cases numerous and more or less united into a tube enclosing the pistil. The carpels may be few, 2-5, and completely united, forming a solid fruit. In some of the Malvaceae they are numerous and separate at maturity into one-seeded pods. There are seven families, mostly tropical. The majority of the temperate species belong to the family Malvaceae. Some of them, e.g., Hibiscus, Althaea, and Sidalcea, have showy flowers and are often cultivated. In the Western States are several characteristic genera.

Other important families of the Malvales are the Tiliaceae, the Bomba; caceae, and the Sterculiaceae. These are mainly tropical or subtropical and have few representatives in the temperate regions. The linden, Tilia, has three species in eastern United States; T. Americana is the basswood.

The Bombacaceae are tropical trees of gigantic size. Among these are the baobab (Adansonia) and the silk-cotton trees (Bombax and Ceiba). Some of these furnish the "kapok" used in upholstery. The famous East Indian fruit, durian (Durio zibethinus), also belongs to the Bombacaceae.

The Sterculiaceae are mostly tropical or subtropical trees, some of which, like the Australian flame tree (Brachychiton acerifolia), have very showy flowers. The only representative of the family in the United States is the Californian Fremontia californica. In the latter, and also in Brachychiton, the corolla is absent, the calyx being petaloid. Several species of Dombeya from South Africa are cultivated in California. The tropical Theobroma cacao furnishes chocolate.

ORDER 12. PARIETALES

This order is a very large one with about fifty families, whose relationships are not always very clear. There is much variation in the floral structures, but in most of them the placentae with the ovules are attached to the wall of the ovary, i.e., the placentae are "parietal."

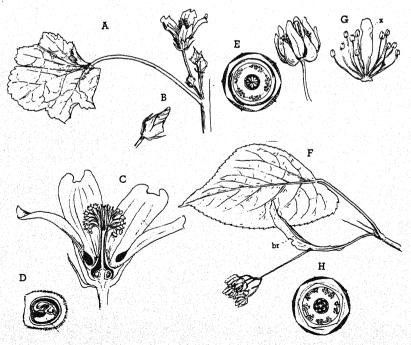


Fig. 338.—A-E, Malva rotundifolia; F-H, Tilia americana; br, bract subtending the inflorescence; G, flower; x, group of stamens.

The calyx and corolla are mostly pentamerous and sometimes the stamens may also be five or ten, but frequently the stamens are numerous. The number of carpels also is variable but most often is three. With few exceptions the flowers are actinomorphic.

Most of the families are unrepresented in the North Temperate Zone. The following families, however, occur in the United States: Theaceae, Guttiferae, Cistaceae, Passifloraceae, Loasaceae, Fouquieraceae, and Violaceae.

DILLENIACEAE

Probably the most primitive forms are the Dilleniaceae, a family largely tropical but also with many species in Australia. In the Australian genus *Hibbertia* the numerous stamens and free carpels recall the floral structure of the Ranales or the lower Rosales. In *Dillenia* the numerous carpels are close together but do not form a true compound pistil. These characters suggest a derivation of the family from ranalean ancestors.

THEACEAE, GUTTIFERAE

The Theaceae include a considerable number of tropical and subtropical trees and shrubs. *Thea*, the type genus, includes the tea plant, *T. sinensis*, as well as the ornamental *Camellia japonica*. In the Southern States are

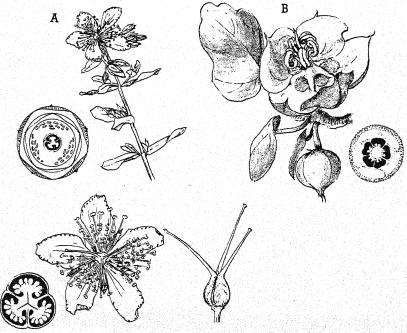


Fig. 339.—A, Hypericum perforatum; B, Fremontia Californica.

two genera, Stuartia and Gordonia. Stuartia is found also in Japan, and species of Gordonia also in India, Asia, and the Malayan regions. They are shrubs or small trees with handsome white flowers. The Guttiferae are almost exclusively tropical in their distribution; but one genus, Hypericum (St.-John's-wort), is a conspicuous exception. This genus of some two hundred species is cosmopolitan and has many species in the North Temperate regions. The showy yellow flowers have conspicuous oil glands, which are characteristic of the family. The stamens are numerous, and often in several groups. There are 3–5 carpels. The ovary may be unilocular or with 3–5 chambers.

Among the characteristic tropical genera are Clusia and Garcinia. Clusia is a large genus of handsome shrubs and trees with large magnolia-like leaves and showy, usually dioecious, flowers. Most species of Clusia begin life as epiphytes, sending down aerial roots, which finally strangle the host and recall the strangling figs of the Eastern tropics. Garcinia has many species in the East Indies, among them the famous mangosteen (G. mangostana), one of the finest tropical fruits.

Hutchinson separates the Guttiferae and several related families as an order, Guttiferales.

FOUQUIERIACEAE

Among the most remarkable plants of the southwestern desert is the "ocotilla," *Fouquiera splendens*, whose clumps of slender stems tipped with a cluster of scarlet flowers are conspicuous features of the landscape. A second genus, *Idria*, grows in Lower California. The relationships of the family are not very clear. It is generally placed next the Tamaricaceae.

CISTACEAE

The type genus, Cistus, has numerous species, especially in the Mediterranean region. They are shrubs with showy, rose-like flowers. Many are cultivated in California and other warm temperate countries. In the United States are a few species of "rockroses," Helianthemum, much resembling Cistus. The other American genera are Hudsonia and Lechea, the latter with insignificant flowers.

VIOLACEAE

A large majority of the species of the Violaceae belong to Viola, which has many species in the United States. Unlike most of the genera of the Parietales, Viola has strongly zygomorphic flowers. The flower is pentamerous, with three carpels, which form a capsule with three parietal placentae. All of the American species are herbaceous perennials.

While the greater number of species of Viola are found in the North Temperate Zone, the genus is cosmopolitan. In Hawaii are several species of Viola which become shrubs five or six feet tall. About a dozen other genera are known. One of these, Isodendron, is peculiar to Hawaii and has flowers which are nearly actinomorphic.

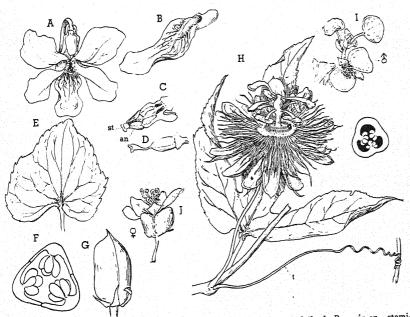


Fig. 340.—A-G, Viola cucullata; H, Passiflora incarnata; t, tendril; I, Begonia sp., staminate flower; J, pistillate flower.

PASSIFLORACEAE

The passionflowers, Passiflora, are mostly tropical climbers, with extremely showy flowers. Besides Passiflora, which contains most of the species, there are several other genera, mostly tropical. Most of the species of Passiflora are American, and several species are often cultivated for their handsome flowers. P. edulis, "passionfruit," and granadilla (P. quadrangularis) bear edible fruit. A few species are native in the Southern States, e.g., P. incarnata and P. lutea.

LOASACEAE

The Loasaceae are entirely American and are best developed in western South America. Some of the species of Loasa from Chile, occasionally cultivated, have stinging hairs, like a nettle. In western United States are several species of Mentzelia, whose showy flowers resemble somewhat those of the cacti, to which they are probably related.

DIPTEROCARPACEAE, CARICACEAE, BEGONIACEAE

Among other notable families of the Parietales may be mentioned the Dipterocarpaceae, the Caricaceae, and the Begoniaceae.

The Dipterocarpaceae are trees, often of great size and very important

for their timber. They are found mainly in the Indo-Malayan regions. They sometimes form extensive forests in northern India and elsewhere. The most important genera are *Dipterocarpus*, *Hopea*, and *Shorea*. Many species are found in the Malay Peninsula and Borneo. The fruit in *Dipterocarpus* has two conspicuous wings, developed from two of the calyx lobes.

The Begoniaceae, with some four hundred species of Begonia, are suffi-

ciently familiar ornaments of the garden and greenhouse.

The Caricaceae include about twenty species. Carica, a genus restricted to tropical America, includes C. Papaya, cultivated everywhere in the tropics for its melon-like fruit, which is greatly esteemed. It is a small tree with a crown of long-stalked, palmately divided leaves, somewhat like those of the castor bean (Ricinus). The plants are dioecious, with the flowers borne in clusters below the crown of leaves. The five petals are completely united in the staminate flower to form a sympetalous corolla. This is less marked in the pistillate flowers. There are ten stamens and five carpels. The structure of the fruit is much like that of the Passifloraceae.

The relationships of the Caricaceae are not very clear. They are usually placed near the Passifloraceae; but the sympetalous flowers and the fruit, as well as the general habit, suggest the Cucurbitaceae. These resemblances

may be merely homoplastic, and are not entirely convincing.

The flowers of the Begoniaceae are very peculiar and are not easily comparable with those of any other order. They are monoecious, the staminate and pistillate flowers differing greatly from each other. The staminate flower has four perianth segments and a cluster of many stamens. The female flower has five perianth leaves and an inferior, three-angled ovary, composed of three carpels.

The species of Begonia are distributed throughout the moist tropics of both hemispheres but are absent from Polynesia and Australia. Some are epiphytes, others are shrubs or low herbaceous plants, and some, like the familiar tuberous begonias, have large tubers from which new shoots are formed each season.

Besides Begonia there are three small genera very much restricted in their range. One of these, Hillebrandia Sandwicensis, is peculiar to Hawaii and is the only representative of the Begoniaceae in Polynesia. The Begoniaceae form an extremely isolated family. They may possibly be related to the Datiscaceae, a small family of Indian and Indo-Malayan plants.

ORDER 14. OPUNTIALES (CACTALES)

The large, very natural family Cactaceae, the only family of the order, is practically restricted to America, the only exceptions being a few species of *Rhipsalis* in Africa. They reach their culmination in the deserts of Mexico and the adjacent areas of the United States, where they form a

very important element in the desert flora. A few species of "prickly pear" (Opuntia) extend into the Northern States, and many are found in South America. In the wetter regions, e.g., Brazil, there are many epiphytic species of Phyllocactus and Rhipsalis and some species of Cereus, e.g., C. triangularis, a "night-blooming Cereus," climbing by means of aerial roots. These epiphytic species do not develop the spines found in the desert types.

With very few exceptions the cacti are quite leafless, or the leaves are reduced to minute scales. The photosynthetic function is relegated to the stems. In the prickly pears the branches are flattened, simulating a thick, broad leaf. In Cereus the stem is cylindrical and fluted. In such species as C. giganteus of the Colorado Desert and in some related Mexican species the plant may be described as a tree. Another type is that of Echinocactus and Mammiliaria, where the plant body is globular or barrel-shaped. In all of these there is the development of an armor of formidable spines.

The most aberrant of the Cactaceae is *Peireskia*, which has functional leaves, like those of the typical dicotyledons. In the seedling of *Opuntia* also two cotyledons are present, but no later functional leaves.

In what may be considered as the more primitive types, e.g., Rhipsalis and Peireskia, the flower has the perianth showing definite calyx and corolla. In most of the cacti, however, the very numerous perianth leaves do not show this differentiation. In all of them the stamens are many. The carpels are indefinite in number but are less numerous in the simpler flowers of Rhipsalis and Peireskia, and in these the number of seeds is much less. The inferior ovary is unilocular, with the parietal placentae bearing many ovules. The fruit in many cases is an edible "berry," sometimes of large size.

Relationships.—The relationships of the Cactaceae are not at all clear. The similarities of the flowers in some of the Loasaceae, especially in Mentzelia and the Cactaceae, make it not unlikely that these two strictly American families are really related.

ORDER 15. MYRTALES

The order Myrtales is mainly tropical or South Temperate in its distribution, but there are some genera characteristic of the North Temperate Zone, especially in the Onagraceae and Elaeagnaceae. Several other families—Thymeliaceae, Lythraceae, and Melastomaceae—have representatives in the United States. The flowers of the Myrtales have the ovary very completely fused with the calyx tube and the floral axis; i.e., the ovary is very decidedly inferior. The perianth is either tetramerous or pentamerous. The stamens may be the same in number as the petals or twice as many; but in the Myrtaceae, the largest family, they are very numer-

ous and the petals may be inconspicuous or absent, the showy red or white stamens replacing the petals as the attractive organs of the flower.

Fossil Myrtales.—There is evidence that the Myrtales existed in the Cretaceous, but there is some question as to their relationships with existing genera. Some of these fossils have been referred to Eucalyptus; there seems to be no question that they belong to the Myrtaceae, but it is at least questionable whether or not they are really species of Eucalyptus. Some Early Tertiary deposits (Eocene) contain fossils believed to belong to the Combretaceae; among them are species of Terminalia.

MYRTACEAE

Myrtaceae, the largest family of the order, has few representatives in the North Temperate Zone and none at all in the United States. All of the species are either trees or shrubs. There are many species in the Eastern tropics, but the family is best developed in South America and in Australia, which has over eight hundred species and where the family ranks second in the flora. The largest Australian genus is *Eucalyptus*, with over two hundred species, some being trees of gigantic size, others shrubs. Many species, especially the "blue gum," *E. globulus*, are planted in all the warm temperate regions, like California, South Africa, southern Europe.

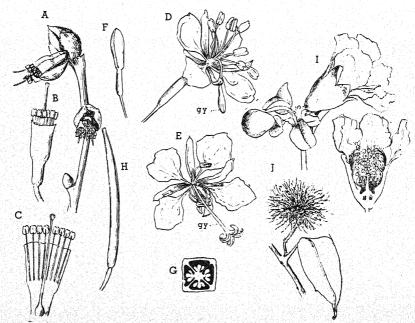


Fig. 341.—A-C, Dirca palustris; D-H, Epilobium spicatum; gy, pistil; I, Punica granatum; J. Eucalyptus leucoxylon rosea.

Other Australian Myrtaceae—Leptospermum, Melaleuca, Callistemon, and Eugenia—are often grown in California.

The largest genus of Myrtaceae is *Eugenia*, which with its closely related genus, *Jambosa*, has species in all tropical countries but especially in South America. Other tropical fruits are the *Guava* (*Psidium*). In the Hawaiian Islands are several species of *Eugenia* and *Metrosideros*.

THYMELIACEAE

This family is cosmopolitan but is represented in the United States by only a single genus, *Dirca*, with two species, one in the Eastern States and one on the Pacific slope. The flowers of the Thymeliaceae are apetalous, but the tubular calyx is petaloid and resembles a sympetalous corolla. To this family belong the species of *Daphne*, often cultivated for their attractive fragrant flowers. Most of the family are shrubs found in the more arid, warm, temperate areas of the Southern Hemisphere, especially Australia.

ELAEAGNACEAE

This is a small family of North Temperate shrubs and small trees which grow mostly in dry regions. The stems and leaves are covered with scurfy scales. There are three genera, of which two, *Elaeagnus* and *Lepargyrea* (*Shepherdia*), are found in northern United States and Canada. *L. argentea* is the "buffalo berry" of the Rocky Mountains.

LYTHRACEAE

The loosestrife family, Lythraceae, is cosmopolitan, and is represented in the United States by almost a dozen species, mostly insignificant herbaceous plants. The type genus, Lythrum, has several species, with rather showy purple flowers. In the warmer parts of the country the very showy crape myrtle (Lagerstroemia) is sometimes seen. The pomegranate (Punica granatium), whose flowers are somewhat similar, belongs to the small family, Punicaceae.

COMBRETACEAE, LECYTHIDACEAE

Some other families of the Myrtales are the mangroves (Rhizophoraceae), and the Combretaceae, including numerous tropical trees and shrubs and some lianas. The Combretaceae are exclusively tropical. *Terminalia catappa*, a characteristic tree of the eastern tropical strand flora, is frequently planted throughout the tropics. *Terminalia* and *Combretum*, the largest genera, have numerous species in both the Old World and the New. *Quisqualis Indica*, a handsome vine, is often grown in conservatories.

The Lecythidaceae are all tropical forms. The Brazil nut, Bertholletia excelsa, one of the largest trees of the Amazon forest, is a member of this family.

MELASTOMATACEAE

This large family has over two thousand species, almost exclusively tropical. They are most abundant in the American tropics, especially in Brazil. There are also many species in the East Indies. They are rare in the temperate zones. In the United States about half a dozen species of *Rhexia* from the southeastern states are the sole representative of the family.

The family includes herbaceous, shrubby, and arborescent species, many with very handsome flowers. The leaves are characteristic, having several longitudinal veins connected by lateral branches. The flowers are mostly pink or purple, and many of them are prized in cultivation. Among these may be cited species of *Tibouchina (Pleroma)* from Brazil, with violet-purple flowers, and *Medinilla*, climbing shrubs, and epiphytes, mostly from the Malayan regions, often seen in greenhouses. The large clusters of rose-colored flowers are often enclosed in showy pink bracts.

HALORAGIDACEAE

The small family Haloragidaceae is composed of herbaceous plants, some of great size. Some of them are aquatics with inconspicuous flowers, e.g., Myriophyllum, a common water plant everywhere. In the Eastern States two other genera, Hippuris and Proserpinaca, are found. The great majority of the species are found in the Southern Hemisphere and belong to Halorrhagis and Gunnera. The latter is best developed in New Zealand and in temperate South America. There is a single species in Hawaii, and another in Costa Rica. In some species the leaves are of gigantic size—sometimes with petioles two yards long—and the lamina of the leaf of corresponding size.

Gunnera shows evidences of being a very primitive type. The embryo sac has 16 instead of 8 nuclei, and the anatomy of the stem suggests the monocotyledons rather than the typical dicotyledons. The geographical distribution of the species also indicates that it is a relict form.

ONAGRACEAE

The largest family of the Myrtales in North America is the Onagraceae, which is especially developed in the Western Hemisphere. *Epilobium* has numerous species in Europe and North America, and the evening primroses (*Enothera*) have species in all parts of the United States. In the Pacific States, Mexico, and the Andean regions are many showy genera, e.g., *Godetia*, *Clarkia*, *Enothera*, *Zauschneria*, and from the mountains of Mexico through South America, many species of *Fuchsia* are found. The last-named genus has three species also in New Zealand.

ORDER 16. UMBELLIFLORAE

The last order of the Dialypetalae includes three families—Araliaceae, Umbelliferae, and Cornaceae. The first two are evidently related, but the relationships of the Cornaceae are not so clear. The usually small flowers are in most cases in umbels. They are almost always epigynous, i.e., have an inferior ovary, and most of them have tetramerous or pentamerous flowers. All of the families are represented in the United States.

ARALIACEAE

The Araliaceae are mostly small trees or shrubs, but most of those in the United States are herbaceous perennials. There are four species of Aralia in the Eastern States, one, A. spinosa (Hercules' club), a small tree, with spiny stems and very large decompound leaves. The other species are herbaceous. Panax quinquefolium is the "ginseng." In the Northwest and in Alaska is Echinopanax horridum, "devil's club." Some of the Araliaceae have dioecious flowers, and there may be numerous stamens, but the number is usually the same as that of the petals. There may be a solitary carpel or many carpels, but usually they are the same in number as the petals. The fruit is berry-like, rarely separating into sections.

The great majority of the Araliaceae are tropical, and they are especially numerous in South America. In Hawaii there are about a dozen species—more than in the whole of the United States. Some of these Hawaiian genera are related to those in New Zealand.

The Araliaceae are very old types. Fossils from the Cretaceous show many forms, and the family is presumably older and more primitive than the Umbelliferae. This is indicated also in the more generalized character of the flowers.

UMBELLIFERAE

The large and cosmopolitan family of the Umbelliferae is extraordinarily uniform in structure. The family belongs essentially to the temperate zones, and is poorly developed in the tropics. They are mostly herbaceous with hollow stems and decompound leaves, with sheathing bases. Rarely (Hydrocotyle) the leaves are undivided. The small flowers are usually borne in symmetrical compound umbels. There are 5 sepals, 5 petals, 5 stamens, and 2 carpels, the latter usually separating into 2 one-seeded fruits (mericarps). The Umbelliferae include several common vegetables—carrot, parsnip, caraway, celery, and fennel—as well as some very poisonous ones, like the poison hemlock (Conium and Cicuta).

CORNACEAE

The dogwood family, Cornaceae, is made up mostly of trees and shrubs, with a majority of the species in the Northern Hemisphere but with several small genera in the South Temperate Zone.

The largest genus is *Cornus*, which has over a dozen species in the United States and has representatives throughout the North Temperate Zone. Two American species, the flowering dogwood of the Eastern States, *C. florida*, and the Western *C. nuttallii*, are among the showiest flowering trees in our territory. *Nyssa sylvatica*, the "pepperidge" ("tupelo," "sourgum"), is a very characteristic tree of the Eastern States. Two or three other species are found in the Gulf region and in southeastern Asia. Most of the other genera are in Asia. *Aucuba Japonica* is common in cultivation. In New Zealand and Chile are several species of small trees or shrubs with handsome evergreen foliage, some of which are cultivated in California.

The flowers, which sometimes are dioecious, e.g., Aucuba, usually have 4 petals, and 4 stamens. The ovary is inferior and is two-celled. Except that the petals are free, the flowers are much like those of the sympetalous families, Rubiaceae and Caprifoliaceae, and it is possible that the Cornaceae are thus intermediate between these families and some Dialypetalae, possibly the Arales.

RELATIONSHIPS OF THE UMBELLIFLORAE

Both the Araliaceae and the Cornaceae are very old families, both being recorded from the Cretaceous. It is not unlikely that the two families were derived from some common ancestral forms. The Araliaceae, in which the stamens and carpels are numerous but indefinite in number, e.g., *Plexandra*, may be assumed to be more nearly like such primitive Choripetalae as the Magnoliales than those genera in which the floral organs are definite in number. There is somewhat the same variation shown in the Cornaceae as in the Araliaceae. On the other hand, the extremely stereotyped character of the Umbelliferae points to a relatively recent and highly specialized family, i.e., it is a specialized derivative of the older and more generalized Araliaceae. The derivation of the sympetalous Rubiales from forms like *Cornus* is at least conceivable.

INTERRELATIONSHIPS OF THE DIALYPETALAE

That the Dialypetalae represent a number of independent phyla seems pretty well demonstrated. In the evolution of the floral structures in all of these phyla there is evident a general similarity, but this trend has gone on independently in many lines of development.

Among the Monochlamydeae the Piperales show evidences of a pos-

sible relationship with the Polygonales, which in turn show similar suggestions of the Centrospermae—which apparently are not at all related to the other Dialypetalae.

As to the interrelationships of the other orders, there is much difference of opinion. There is general agreement that the Ranales (Polycarpicae) are among the most primitive forms, but it is not likely that all the dicotyledons can be traced back to the ranalean type; while from this apocarpous type many of the more specialized flowers may have developed, it is pretty certain that this cannot apply to all of them.

The progression from the ranalean type has been toward stability in the number of the floral parts; next, cohesion of the perianth into calyx and sympetalous corolla; syncarpy; and epigyny (i.e., cohesion of the ovary with the floral axis). The primitive actinomorphy is replaced by zygomorphy and is often accompanied by an abortion of some of the stamens. But some of the conditions, assumed to be late in the development of the flower, are met with in some of the oldest-known types. Thus in some of the willows there are definitely two stamens and a syncarpous ovary. In Juglans there is an inferior ovary. It seems hardly likely that such flowers as these have been derived from the ranalean type and that there has been but one phyletic line.

In a good many of the existing orders there may be retained certain primitive characters combined with presumably specialized ones. The Myrtales may be cited. The Myrtaceae are known to be very old; but many of them, e.g., Eugenia and Eucalyptus, have retained the numerous stamens, with the inferior ovary. The derivation of the myrtaceous flower from the ranalean one seems highly improbable, and the same might be said for other orders, e.g., Geraniales, Rhamnales, and others, where there is rarely any evidence of derivation from a ranalean type but rather from some simple forms of Monochlamydeae.

Zygomorphy has undoubtedly developed independently many times, and is presumably associated with entomophily. It may even occur in the primitive Ranunculaceae, e.g., *Delphinium*, *Aconitum*; in the Geraniaceae, e.g., *Pelargonium*; and in Leguminosae. In short, the Dialypetalae may be assumed to represent many independent phyla in which there has been a more or less similar tendency in the evolution of the floral structures. These resemblances, however, are homoplastic, not homologous.

CHAPTER XXVII

ANGIOSPERMS—DICOTYLEDONS: SYMPETALAE (METACHLAMYDEAE)

The third division of the dicotyledons, the Sympetalae, includes the majority of the angiosperms and the most recent and specialized forms of the dicotyledons; thus they may be said to stand at the head of the vegetable kingdom.

As the name indicates, the characteristic feature is the sympetalous (gamopetalous) corolla, which, however, is not universal, as some members of the more primitive families, like the Pirolaceae, Clethraceae, Oleaceae, have the petals nearly or quite free and indicate a derivation from some Dialypetalae. Among the latter, on the other hand, are genera with true sympetalous flowers, e.g., Fouquiera and the Cucurbitaceae. The latter, often placed in the Sympetalae, have both sympetalous and choripetalous genera. It is clear then that the line between the Dialypetalae and the Sympetalae is a very indefinite one.

There is much less range of structure in the flowers of the Sympetalae, compared with the Dialypetalae, and the number of orders and families is smaller. With very few exceptions, e.g., *Diospyros*, the stamens are never more than twice as many as the corolla lobes, and frequently there is a suppression of one or more—e.g., in the Labiatae and the Scrophulariaceae. This is frequently associated with marked zygomorphy, a condition evidently associated with insect pollination.

The flowers may be either hypogynous or epigynous, and the carpels and stamens may be equal in number (isocarpous), but as a rule the number of carpels is reduced (anisocarpous). The ovules have only a single integument. Based on the number of carpels, the Sympetalae are sometimes divided into "Isocarpae" and "Anisocarpae"; but this division is a somewhat artificial one.

The majority of the Sympetalae in temperate regions are herbaceous annuals or perennials, but there are some trees and shrubs and occasionally woody climbers, like the honeysuckles (Lonicera) and the trumpet creepers (Tecoma and Bignonia). Among the native American trees there are also the catalpa, ash, and persimmon of the southeastern states and the madroño (Arbutus) of the Pacific Coast. Among the common shrubs are the rhododendrons, the huckleberries, manzanita (Arctostaphylos), Viburnum, and elder (Sambucus). There are a good many shrubby spe-

cies in the mild climate of the Pacific Coast whose Eastern relatives are herbaceous. In the subtropical and tropical zones there are a great many sympetalous trees and woody lianas.

CLASSIFICATION OF SYMPETALAE

The Sympetalae, like the Dialypetalae, probably represent several phyla derived independently from choripetalous ancestors. Thus Wettstein connects two orders, Primulales and Plumbaginales, with the Centrospermae; the Rubiales with the Umbelliflorae; and the Ericales (Bicornes) with the Guttiferales. Engler recognizes eight orders and Wettstein ten; but they differ as to the scope of these orders. Thus two orders, Plumbaginales and Primulales, of Wettstein are united into one by Engler. Both of these show marked similarities to the Centrospermae, perhaps the most primitive order of the Choripetalae.

The eight orders of Engler are: (1) Primulales; (2) Ericales; (3) Ebe-

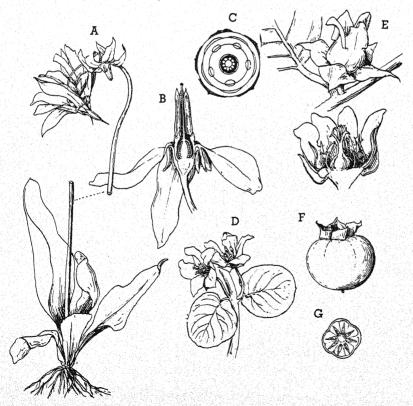


Fig. 342.—A-C, Dodecatheon Meadia; D, Lysimachia nummularia; E-G, Diospyros virginiana.

nales; (4) Contortae; (5) Tubiflorae; (6) Plantaginales; (7) Rubiales; and (8) Campanulatae. Of these the first three are isocarpous, the others anisocarpous. To these Wettstein adds Plumbaginales and Ligustrales.

ORDER 1. PRIMULALES (INCLUDING PLUMBAGINALES)

The Primulales resemble the Centrospermae, perhaps the most primitive of the Choripetalae, in the structure of the ovary, which is unilocular with basal placenta. In the Plumbaginales there is a single basal ovule, thus resembling *Chenopodium* and *Amaranthus*; in the Primulaceae as in the Caryophyllaceae the central placenta has numerous ovules.

The Primulales show no evidences of relationship with any other order of the Sympetalae. There are three families. The Plumbaginaceae are cosmopolitan, but the majority are tropical or subtropical. Very few species occur in the United States.

The Primulaceae also are cosmopolitan but are best represented in the North Temperate Zone, where the large genus *Primula* has many species. There are many species also in the higher mountains of the Eastern tropics; thus in western Java, the handsome *P. imperialis* grows at an elevation of 10,000 feet. The flowers of the Primulaceae are mostly pentamerous. In some species the flowers are "dimorphic," i.e., there are two floral types, one with elongated style and stamens at the bottom of the corolla tube, the other with short style and stamens at the top. This insures cross-pollination, as the flowers are sterile to their own pollen.

Other characteristic genera are Anagallis, Trientalis, Cyclamen, Dode-catheon, and Lysimachia. In these the corolla has almost no tube, the petals are nearly separated, the open flower appears to be choripetalous.

The third family, Myrsinaceae, are almost exclusively tropical and subtropical trees and shrubs, with many species in the American and Asiatic tropics. Some species reach Japan, Mexico, and southern Florida and in the Southern Hemisphere extend to New Zealand and the Cape region.

ORDER 2. ERICALES (BICORNES)

The Ericales include both choripetalous and sympetalous genera and to some extent occupy a position intermediate between the Choripetalae and the Sympetalae. Wettstein connects them with the Guttiferales. The order as a whole, like the Primulales, seems to be quite unrelated to the other Sympetalae.

The family Clethraceae, mostly tropical, has two species in the Atlantic States. Clethra alnifolia is the "sweet alder." The flowers are choripetalous. The Pirolaceae are exclusively boreal, some of them reaching beyond the Arctic Circle. Some of the species, e.g., Pirola rotundifolia and P. (Moneses) uniflora, are circumpolar. These have free petals; and this is the case also in Monotropa. The latter genus and several others comprise the

subfamily, Monotropeae, and are root parasites or saprophytes, having no chlorophyll. *Monotropa uniflora* is the "Indian pipe" or "ghost flower," of the northern states. *Pterospora*, a root parasite, and *Sarcodes Sanguinea*, the snow plant of the Sierra Nevada, have sympetalous corollas.

The Ericaceae, one of the largest families of the angiosperms, is cosmopolitan and includes many familiar shrubs and some prostrate forms, like the cranberries and the trailing arbutus (*Epigaea*). They are best developed in the temperate regions of both the Northern and Southern hemispheres, but there are a good many, mostly mountain species, in the tropics. Among them are many very showy flowers, like the rhododendrons, the azaleas, *Kalmia*, and many species of heather (*Erica*). They are often gregarious and may cover large areas, like those on the moors in Europe, and the cranberries, huckleberries, and *Ledum* in America.

The hypogynous corolla is typically actinomorphic and sympetalous, often urn-shaped. In a few cases, however, e.g., *Ledum*, the petals are separate, as they are in some of the Pirolaceae. The flowers are usually pentamerous, with 5 or 10 stamens, and the same number of carpels. The genus *Rhododendron* (inc. *Azalea*), next to the largest in the family, has

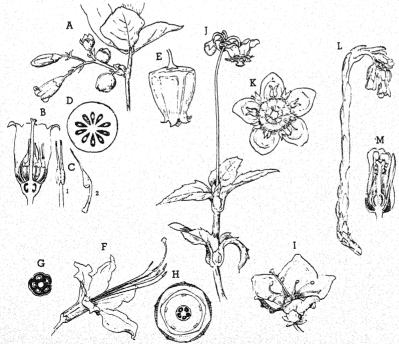


Fig. 343.—A-D, Gaylussacia resinosa; E, flower of Oxydendrum arboreum; F-H, Azalea canescens; I, Kalmia latifolia; J, K, Chimaphila maculata; L, M, Monotropa Hypopitys.

many very beautiful species, especially in the Himalayas, China, and Japan. There are also epiphytic species in the East Indies. Some very beautiful species grow in both eastern and western United States. The beautiful "mountain laurel," Kalmia, and the "arbutus," Epigaea, are members of this family. The largest genus, Erica, belongs exclusively to the Old World. These heaths are especially developed in the Mediterranean countries and even more so in South Africa. Many handsome species from the Cape are prized in cultivation.

Another large genus, Vaccinium, furnishes edible fruits, e.g., huckleberries, cranberries. Most of these are northern types, but there are

numerous species in the tropical mountain forests.

A characteristic tree of the Pacific Coast is the madroño (Arbutus Menziesii), and several species of manzanita (Arctostaphylos) are very common. There are few Ericaceae in the Southern Hemisphere, except in South Africa. In the Australasian region there are several species of Gaultheria, related to the "wintergreen" (G. procumbeus) of eastern United States, and the "salal" (G. shallon) of the Pacific Coast. For the most part the Ericaceae are replaced in the Southern Hemisphere by a related family, the Epacridaceae, heath-like shrubs, of which the majority are in Australia. Others occur in New Zealand, South America, Indo-Malaya, and Hawaii.

ORDER 3. DIOSPYRALES (EBENALES)

The Diospyrales are mostly tropical trees or shrubs. There are four families: Sapotaceae, Ebenaceae, Styracaceae, and Symplocaceae. The only representative in the United States of the Ebenaceae is the persimmon, Diospyros virginiana. The other families have a few species, mostly in the Southern States, e.g., Bumelia (Sapotaceae), Halesia, Styrax (Styracaceae), and Symplocos (Symplocaceae).

The flowers are in many cases dioecious. In the common persimmon the corolla is tubular with four lobes. In the pistillate flower there are 8 imperfect stamens; in the staminate, 16 fertile stamens. There may some-

times be perfect flowers also. The ovary is 8-celled.

In Symplocos the stamens may be very numerous, and in the Styracaceae the petals are nearly or quite free. These characters as well as the occurrence of diclinous flowers in many cases suggest a relationship with the more primitive Choripetalae.

Some of the Diospyrales are of economic importance. The persimmons are valued for their fruit, and the valuable cabinet wood, ebony, is obtained from *D. ebeneum*. The Sapotaceae have a milky latex from which rubber is produced, and *Achras sapota* is important to the American public as the source of "chicle," the basis for chewing gum.

Wettstein groups the Diospyrales with three other orders—Contortae, Tubiflorae, and Ligustrales—in a series indicating a certain degree of relationship.

ORDER 4. CONTORTAE

The Contortae include about half a dozen families, mostly cosmopolitan in distribution. The flowers are actinomorphic and the corolla lobes mostly twisted (convolute) in the bud, although there are many exceptions. There are two carpels, which may become separate in fruit but more commonly form a unilocular or bilocular ovary.

In the lowest family, Oleaceae, sometimes placed in a separate order, Ligustrales, the petals may be entirely free or even absent; but in general the corolla of the Contortae is strictly sympetalous. The order has both herbaceous and woody types, including some large trees. The principal families are Oleaceae, Loganiaceae, Gentianaceae, Apocynaceae, and Asclepiadaceae.

OLEACEAE

The large family Oleaceae has but few native American species, the most important being several species of ash (Fraxinus). The olive (Olea europaea) is the most important cultivated species, and several shrubs and vines from Europe and eastern Asia are prized for their showy flowers. Various species of lilacs (Syringa), privet (Ligustrum), Jasminum, and Forsythia are familiar examples.

LOGANIACEAE

The Loganiaceae are with few exceptions tropical forms, with few species native to the United States. The best known is the Southern "jasmine" (Gelsemium sempervirens), a handsome evergreen creeper with fragrant yellow flowers.

A genus of trees and shrubs and lianas found in the tropics of both hemispheres is *Strychnos*. These have poisonous seeds; one of them, *S. nux-vomica*, yields strychnine. Another widespread genus is *Buddleia*, cultivated for their handsome flowers.

GENTIANACEAE

The Gentianaceae are mostly herbaceous plants, the largest genus, Gentiana, with many showy species in most parts of the world except Africa. They are especially abundant in the mountains of Europe and extend to Greenland and Spitzbergen. Other American representatives are Erythraea, Halenia, Bartonia, Menyanthes, and Sabbatia, the last restricted to eastern and southern United States.

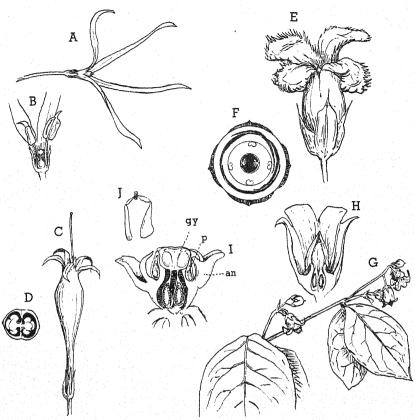


Fig. 344.—A, B, Chionanthus virginica; C, D, Spigelia marylandica; E, F, Gentiana crinita; G, H, Apocynum androsaemifolium; I, section of flower of Asclepias syriaca, showing the stigma, gy, and pollinium, p; I, pair of pollinia, with adhesive connecting body.

APOCYNACEAE

The Apocynaceae, a large family of mostly tropical trees, shrubs, and lianas, has a few representatives in the temperate zones, including the type of the order, Apocynum (dogbane), with two common species in the United States. The only other genera represented are Amsonia, Cycladenia, and Trachelospermum, with three or four species. In the tropics of both the Old World and the New are many species with very showy flowers; and a considerable number in the temperate zones, both north and south, reach beyond the tropics.

The leaves are opposite and entire, and all the members of the family develop milky latex, which in some of them yields excellent rubber. Several species of *Landolphia* in West Africa are the principal source of native rubber. The latex in some of the Apocynaceae, e.g., oleander, is poisonous.

The flowers are tubular or bell-shaped, with five corolla lobes, which are twisted (convolute) in the bud. There are five stamens and generally two carpels, which sometimes are separate but more commonly united.

Owing to the showy and often fragrant flowers, some of them are favorite garden plants where the climate permits. From southern Europe come the oleander (Nerium) and the periwinkles (Vinca). In California the handsome vine, Mandevilla suaveolens, from Argentina is often grown and also the fragrant "Malayan jasmine," Trachylospermum jasminoides, from Japan. In tropical gardens and in greenhouses showy species of Allamanda and Plumiera are common.

ASCLEPIADACEAE

This is the largest and the most specialized family of the Contortae. They are evidently closely related to the Apocynaceae, with which they agree in the essential structure of the flowers, the general habit, and the presence of a milky latex.

There are over two hundred genera, some small, even monotypic, but others, e.g., Asclepias, with probably a hundred species. They are cosmopolitan, but the larger number are in the tropical regions, only a few relatively being extra-tropical. The most marked exceptions are in South Africa, where there are about four hundred species. The Asclepiadaceae are most numerous in the Eastern Hemisphere, but there are many peculiarly American genera and only a few genera like Asclepias occur in both hemispheres.

The flowers are remarkably uniform in structure. They are hypogynous and pentamerous, and always have two free carpels, which generally develop into inflated follicles. The seeds almost always have tufts of silky hairs and are readily distributed by wind. The corolla may be tubular or "rotate." In the milkweeds (Asclepias) the corolla is deeply cleft and the segments are reflexed. At the case of each of the corolla lobes, there is a conical body, and these constitute the "corona." In Asclepias the five stamens are united into a tube surrounding the carpels, which have a common broad stigma. The anthers are adherent to the stigma, thus forming a "gynostemium," recalling that of the orchids. The corona is composed of five conical bodies, which are nectaries, and these surround the gynostemium. The pollen is in masses, "pollinia," like those in the orchids and can be removed from the anthers only by insects. The pollinia are in hairs connected by a sticky "translator," which adheres to the legs of the butterfly or bee, the pollinia thus being withdrawn and transferred to the receptive stigma of another flower. A similar mechanism is found in many other Asclepiadaceae.

Asclepias is represented by numerous species in the United States and Mexico. Except for a few species in Africa the species are all American.

Among the cultivated members of the family are Stephanotis and Physianthus (Araujia) with fragrant white flowers. Among the most remarkable of the Asclepiadaceae are some of the South African desert species, some of which are, like Hoodia and Stapelia, fleshy leafless plants, resembling cacti. Of these the genus Stapelia is characteristic. The conspicuous flowers are dull purplish in color, and have a fetid odor supposed to be attractive to carrion-feeding insects.

ORDER 5. TUBIFLORAE

This large order, with about twenty families, includes many familiar sympetalous flowers. The flowers with very few exceptions are pentamerous. In most of them the number of carpels is 2–4. The stamens may be reduced to 2 or 4, especially in the zygomorphic types. The stamens are inserted on the tube of the sympetalous corolla. They are typically hypogynous, but there are some exceptions, e.g., some Gesneraceae. The majority of the families are represented in the temperate zones, and the following families occur in the United States: (1) Convolvulaceae; (2) Polemoniaceae; (3) Hydrophyllaceae; (4) Borraginaceae; (5) Verbenaceae; (6) Labiatae; (7) Solanaceae; (8) Scrophulariaceae; (9) Lentibulariaceae; (10) Bignoniaceae; and (11) Acanthaceae.

In the first four families the flowers are actinomorphic, with five perfect stamens; in the remaining orders, except the Solanaceae, the flowers are almost always zygomorphic, stamens being reduced to 2 or 4. In the Solanaceae the majority are actinomorphic with five perfect stamens, but there are some zygomorphic genera, like Salpiglossis, which have zygomorphic corollas and only four functional stamens.

Most of the temperate species of Tubiflorae are herbaceous annuals or perennials, but in the warmer regions they may develop into trees, like Catalpa and Paulownia, or shrubs. In the tropics are many trees, e.g., Tectona (teak), Spathodea, Crescentia, and many others. There are many showy woody "lianas," like the trumpet creepers, Tecomaria, Bignonia,

and others.

CONVOLVULACEAE

The Convolvulaceae, the morning-glory family, are mostly tropical. The largest genus, *Ipomoea*, includes the familiar morning-glories grown as annuals in gardens, but with many tropical perennial species. The type genus, *Convolvulus*, is more characteristic of temperate regions. *C. arvensis*, a European species, is a troublesome weed. *Ipomoea* has a few species in the United States, e.g., *I. pandurata*, a perennial species with an enormous tuberous root from which the annual shoots are developed. The sweet potato, *I. Batatas*, has similar tuberous roots. There are several native species of *Convolvulus*, especially in California.

Also belonging to the Convolvulaceae are the "dodders," *Cuscuta*, a genus of extreme parasites, often causing great damage to the host plants. They are quite leafless and destitute of chlorophyll. The yellow or reddish twining stems send haustoria into the host plant.

POLEMONIACEAE AND HYDROPHYLLACEAE

The two families Polemoniaceae and Hydrophyllaceae have their greatest development in North America, especially in the Pacific Coast region. Among the characteristic genera are *Phlox*, *Nemophila*, and *Gilia*, common garden plants.

BORRAGINACEAE

The Borraginaceae are cosmopolitan but are best developed in the North Temperate Zone. They are most abundant in the Mediterranean countries, but there are many species in the California area. Some of them are cultivated, e.g., forget-me-not (Myosotis), heliotrope, and Echium. The flowers are much like those of the Hydrophyllaceae, and are borne on a one-sided coiled ("scorpioid") raceme. The four carpels separate into as many "nutlets," which in some forms are covered with hooked appendages by which they adhere to the coat of animals, including human beings,

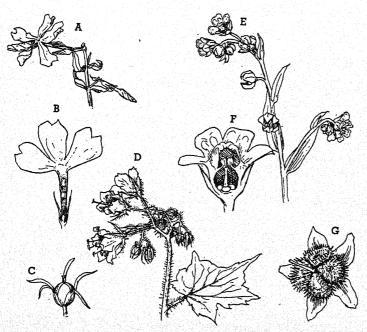


Fig. 345.—A-C, Phlox divaricata; D, Hydrophyllum appendiculatum; E-G, Cynoglossum officinale.

and are thus distributed. Among the widespread genera are Mertensia, Cynoglossum, and Lithospermum.

VERBENACEAE

The Verbenaceae are mostly tropical and subtropical plants and are poorly represented in the United States. The genus *Verbena* has a number of species, especially in the Southwest. The garden verbenas are from Argentina, Brazil, and Chile. Some of the tropical Verbenaceae are trees. The most important of these is the teak, *Tectona grandis*, from India and Malaya.

The floral structure of the Verbenaceae resembles that of the Borraginaceae, but the flowers are usually zygomorphic and one of the stamens is suppressed.

LABIATAE

The largest family of the Tubiflorae is the Labiatae, the mint family. This cosmopolitan family has many representatives in the temperate regions. They are mostly herbaceous, but there are a good many shrubby species, like lavender, rosemary, Salvia, from warmer regions. They have square stems with opposite leaves, and very generally an aromatic scent. The floral structure is very uniform. The zygomorphic corolla is two-lipped and the stamens may be reduced to two or, if four, they are "didynamous," i.e., two long and two short. As in the Borraginaceae, the fruit is composed of four "nutlets."

SOLANACEAE

The nightshade family, Solanaceae, is a large one, cosmopolitan in distribution but best developed in the American tropics. The family is of great importance economically, as it not only furnishes such important food plants as the potato and tomato but also includes a number of genera which are poisonous but from which such important drugs as atropin, nicotine, and others are obtained. Among the most important of these plants are Atropa belladonna, tobacco (Nicotiana), stramonium (Datura).

The majority of the Solanaceae, e.g., Solanum and Petunia, have actinomorphic flowers, pentamerous, with the carpels forming a compound ovary. The general structure is perhaps most like the Polemoniaceae or the Convolvulaceae. There are, however, exceptions, like Salpiglossis and Browallia, which have zygomorphic flowers and only four stamens, much resembling in appearance the flowers of the Scrophulariaceae and suggesting a connection between the latter and the actinomorphic members of the Solanaceae.

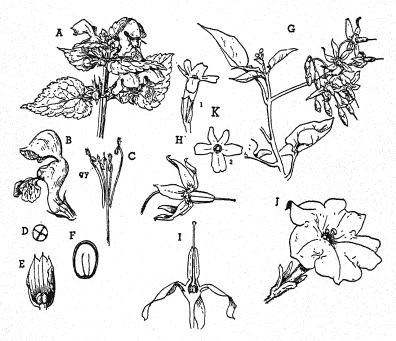


Fig. 346.—A-F, Lamium album; G-I, Solanum dulcamara; J, Petunia sp.; K, Verbena hastata.

SCROPHULARIACEAE

The Scrophulariaceae reach their greatest development in the North Temperate Zone, and their numbers diminish toward the Equator. They are also less developed in the Southern Hemisphere. In North America they reach their maximum development in the Rocky Mountains and on the Pacific Coast, where certain genera, like Pentstemon, Castilleia, and Mimulus, have many showy species. They are for the most part herbaceous, but in the milder climates like California and New Zealand there are some shrubby species, e.g., the Californian Antirrhinum speciosum, and numerous shrubby species of Veronica in New Zealand.

The flowers are more or less strongly zygomorphic and usually have four stamens. Rarely there are five, e.g., *Verbascum*, and in *Veronica* only two. The snapdragon (*Antirrhinum*) and foxglove (*Digitalis*) are familiar garden flowers.

Some of the Scrophulariaceae are partial root parasites. Some species of the American genera, Castilleia and Gerardia, have this habit.

LENTIBULARIACEAE

The Lentibulariaceae are probably related to the Scrophulariaceae, and the flowers have much the same structure. They are aquatic on bog plants, and like the Droseraceae are truly carnivorous. The principal genera are *Utricularia*, "bladderweed," and *Pinguicula*, "butterwort." The common species of *Utricularia* are submersed aquatics with finely divided leaves bearing characteristic vesicles equipped with an extraordinary apparatus for the capture of small organisms. *Pinguicula*, growing in boggy places, has broad leaves covered with glands secreting an adhesive substance, somewhat like *Drosera*, by which small insects are trapped as the leaf margins fold over the victim.

In tropical America are some remarkable species of *Utricularia*. *U. montana*, found in Trinidad, is an epiphyte and has beautiful large white flowers looking like an orchid. Another South American species, *U. nelumbifolia*, lives in water collected between the leaf bases of some

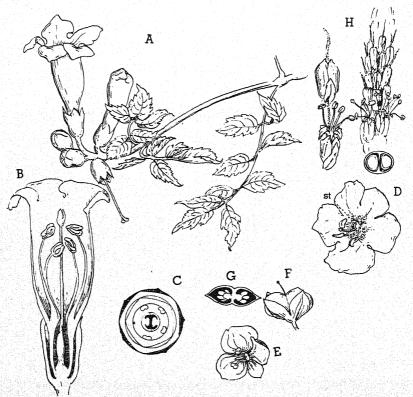


Fig. 347.—A-C, Tecoma radicans; D, Verbascum blattaria; st, sterile stamen; E-G, Veronica scutellata; H, Plantago major.

of the large terrestrial bromeliads. The submerged branching stems develop traps like those of the ordinary bladderweeds, but there are also long-stalked, floating leaves, like a small water-lily leaf, and large violet-purple flowers.

BIGNONIACEAE

The Bignoniaceae are for the most part tropical or subtropical trees or woody climbers, often with very showy flowers. A few species extend beyond the tropics, and in the Southern States there are several species like the trumpet creeper—Tecoma (Campsis) radicans and Catalpa. A single species, Chilopsis linearis, the "desert willow," is found in southern California. The family reaches its greatest development in the American tropics, where many species of Bignonia, Tecoma, and other genera are conspicuous features of the floras. Where the climate permits, e.g., in Florida and California, several showy species from South America, South Africa, and Australia are cultivated—Jacaranda mimosaefolia, Tecomeria capensis, Pyrostegia ignea ("Bignonia venusta"), and others.

GESNERIACEAE

This large family has no representatives in the United States, but has many species in the tropics of both hemispheres and includes some showy cultivated plants, especially the florists' "gloxinias" (Sinningia). The flowers are structurally much like those of the Scrophulariaceae; and, like the latter, the Gesneriaceae are predominantly herbaceous.

ACANTHACEAE

The Acanthaceae are mostly tropical forms, but a few extend into the warm temperature regions. A few species are found in the Southern States and one is in California. In the Mediterranean region are also several genera, including the type genus, *Acanthus*, sometimes cultivated as an ornamental plant in California. Several species of *Thunbergia* are also in cultivation.

The Acanthaceae are for the most part herbaceous or small shrubs and grow under very varied conditions, some being marsh plants and others growing in extremely arid places. They are perhaps most nearly related to the Bignoniaceae. The leaves are opposite, and the flowers are much like those of the Scrophulariaceae or the Bignoniaceae.

OROBANCHACEAE

Probably related to the Gesneriaceae is a small family of extreme parasites, the Orobanchaceae. These are root parasites having no chlorophyll and popularly known as "cancerroot," "broomrape." The principal genus is *Orobanche*, with several species in California. In the Eastern States there are only two species, the commonest, *Epifagus virginiana*, being parasitic on the roots of the beech.

ORDER 6. PLANTAGINALES

Sometimes included in the Tubiflorales, but also regarded as representing an independent order, is the family Plantaginaceae. All but two of the two hundred or more described species belong to the cosmopolitan genus, *Plantago*, including *P. major*, the common plantain, and several other weeds. The genus is best developed in the temperate zones. The relationships of the Plantaginaceae with the other orders is not very clear, and they are generally believed to be reduced forms, derived from some more specialized types of the Tubiflorales, perhaps the Solanaceae or the Scrophulariaceae. The inconspicuous flowers are borne in dense spikes and may be either hermaphrodite or diclinous.

ORDER 7. RUBIALES

The Rubiales, like the Ericales, show no close relationship with the other sympetalous orders and appear to have originated independently from some choripetalous ancestors. There are marked resemblances to the Cornaceae of the Umbelliflorae, which may perhaps indicate a genetic relationship.

The flowers are mostly of moderate size and often are in crowded inflorescences. This is especially marked in the Dipsacaceae, where there is a decided suggestion of the Compositae. The flowers are almost always hermaphrodite. The epigynous corolla may be tubular or urn-shaped, or with a narrow tube and salver-shaped "limb." They are most commonly actinomorphic but may be zygomorphic. They are most commonly pentamerous, but there are many exceptions. The stamens are for the most part the same in number as the corolla lobes. The ovary is syncarpous, usually bilocular; but there are many exceptions. The Rubiales include herbaceous plants and also many woody species. The leaves are typically opposite, with or without stipules. There are five families, of which the Rubiaceae is much the largest, and includes a large majority of the species. The other families are Caprifoliaceae, Adoxaceae, Valerianaceae, and Dipsacaceae.

RUBIACEAE

The family Rubiaceae is very large, including five thousand or more species, with about three hundred fifty genera. The great majority are tropical and constitute a very important element in the vegetation, in both the Eastern and the Western tropics. The tropical species are mostly trees or shrubs.

Less than a dozen genera are found in the United States. The largest, with about fifty species, is *Galium* (bedstraw), herbaceous plants, with straggling rough branches and a small, white, four-parted corolla. Other genera are *Houstonia* (bluets), *Cephalanthus* (buttonbush), and *Mitchella*

(partridgeberry). Except for Galium, which has leaves in whorls, the leaves are opposite and stipulate.

With few exceptions the flowers of the Rubiaceae are actinomorphic. The fruit shows much variation. It may be a fleshy berry, e.g., coffee and *Mitchella*; or the carpels may separate, forming individual, seed-like, dry fruits.

The individual flowers are sometimes showy and in many cases fragrant, e.g., Gardenia. More often they are in more or less dense inflorescences and the individual flowers are relatively inconspicuous. Sometimes where the flowers are inconspicuous, certain individual flowers have one of the sepals developed in a large and conspicuous petaloid leaf. A curious fact is that this peculiarity is found in two not closely related genera: one, Mussaenda, in the Old World tropics; the other, Warsciwiczia, from the West Indies. In Mussaenda the calyx appendage is white, in Warsciwiczia scarlet; possibly the latter may be associated with pollination by humming-birds.

Among the ornamental cultivated Rubiaceae, Gardenia and Bouvardia

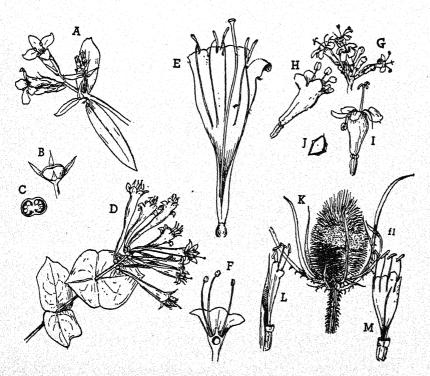


Fig. 348.—A-C, Houstonia purpurea; D, E, Lonicera sempervirens; F, Viburnum sp.; G-I, Valeriana officinalis; K-M, Dipsacus sylvestris.

are the most familiar. Two genera are of great economic importance, viz., Coffea and Cinchona. The former includes about twenty-five species, principally African. C. arabica is Abyssinian; C. liberica is from western Africa; Cinchona, the source of quinine, is peculiar to the Andean regions but at present the commercial supply comes mainly from Javanese plantations.

CAPRIFOLIACEAE

The Caprifoliaceae are mostly shrubs, some of them having twining stems. They are especially characteristic of the Northern Hemisphere and are well represented in the United States. Several species of *Viburnum* are found in the Andean regions and two of *Sambucus* in Australia.

The floral structures are much as in the Rubiaceae. The corolla is usually actinomorphic, but in some species of honeysuckles (Lonicera)

it is decidedly two-lipped.

All but three of the ten genera occur in the United States. Among these are the honeysuckles (Lonicera), snowberry (Symphoricarpos), twinflower (Linnaea), snowball (Viburnum), and elder (Sambucus). The fruit is usually a berry or drupe but may be a dry capsule.

ADOXIACEAE

This small family has a single species, Adoxia Moschatellina, a small herbaceous plant from the northern parts of Eurasia and North America. In habit it suggests the Ranunculaceae, the ternately divided leaves being very different from those of the other Rubiales, and it is possible it should be placed in that order. It is sometimes included in the Caprifoliaceae.

VALERIANACEAE

This family has few representatives in the United States, where there are about a dozen species, belonging to three genera, *Valeriana*, *Valerianella*, and *Plectritis*; the latter is restricted to the Pacific Coast. The family is best developed in the Mediterranean regions.

The great majority belong to *Valeriana*, which has a very wide distribution and has many species in the Andean region of South America and the southern part of the continent. No members of the family are known from Australia or South Africa.

The flower in the Valerianaceae is tubular and may be actinomorphic, or somewhat zygomorphic. The stamens are fewer in number than the (five) corolla lobes. The ovary is inferior and trilocular; but only one carpel is fertile, the fruit has but a single seed, and resembles the "achene" of the Compositae. This resemblance is increased by the development of a tuft of hairs from the margin of the calyx, very much like the "pappus" of the composite fruit. The European Valeriana officinalis is common as a garden plant, and also the red-flowered Centranthus ruber.

DIPSACACEAE

The last family of the Rubiales, Dipsacaceae, the teazle family, is entirely wanting in America. It is especially developed in the temperate parts of Eurasia, especially the Mediterranean regions, but is absent from most of eastern Asia and has no representatives in the Southern Hemisphere. In the United States, the teazle, Dipsacus sylvestris, is a common weed introduced from Europe, and species of Scabiosa are well known as garden flowers.

The Dipsacaceae seem to be pretty closely related to the Valerianaceae, and the structure of the flowers is much the same. The tubular corolla is zygomorphic, with four or five segments and four stamens. The inferior ovary is unilocular, and the fruit, like that of the Valerianaceae, closely resembles the achene of the Compositae and is crowned with a definite pappus.

The similarity of the Dipsacaceae to the Compositae is emphasized by the inflorescence where the flowers are densely crowded and the inflorescence subtended by a circle of bracts, resembling the involucre of the composite "capitulum." The resemblance is especially marked in *Scabiosa*, where the marginal flowers of the inflorescence are much larger than the

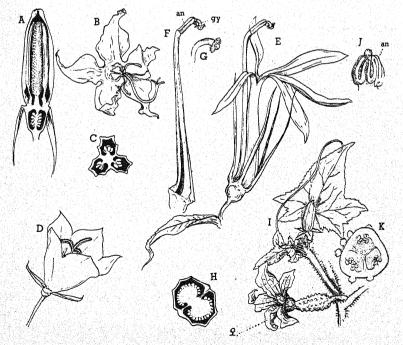


Fig. 349.—A-C, Campanula americana; D, C. carpatica; E-H, Lobelia cardinalis; I-K, Cucumis sativus.

central ones and might be compared to the ray florets of a sunflower. Whether these resemblances indicate a real relationship or are only homoplastic must remain uncertain.

ORDER 8. CAMPANULATAE

The remaining six sympetalous families are placed in a single order, Campanulatae, by Engler. Wettstein makes the first of these families, Cucurbitaceae, the type of an order, Cucurbitales; and the remaining five form the order Synandrae. Both Cucurbitales and Synandrae Wettstein derives from the choripetalous Parietales.

CUCURBITACEAE

The melon family, Cucurbitaceae, is a very natural one, with many species especially in the drier tropical and subtropical countries. Innumerable varieties of melons, cucumbers, squashes, and gourds have been cultivated from ancient times, and their origins are very uncertain. The melons are Old World plants, but the pumpkins and squashes (Cucurbita pepo) are believed to be of American origin, as they were cultivated by the Indians before America was discovered.

About a dozen wild species of Cucurbitaceae are found in the United States. The wild cucumbers (*Echinocystis* spp.) are found in both the Atlantic and the Pacific states. They are rapidly growing herbaceous vines, climbing by tendrils. The California species have an enormous tuberous root from which are sent up the annual shoots. The flowers of the Cucurbitaceae are mostly diclinous, either monoecious or dioecious. The flowers are usually pentamerous, and the corolla as a rule is sympetalous; but there are some genera with petals nearly or quite distinct. The stamens are free in some cases, but as a rule the stamens are united and the anthers are much elongated and coherent, forming a "synandrium."

The relationships of the Cucurbitaceae with other families are very obscure. While they are usually placed next the Campanulaceae, it is evident that the relationship, if any, must be remote. It has also been thought that they might be related to the choripetalous families Passifloraceae, Loasaceae, and Begoniaceae. It is also possible that the Papayaceae might be considered as relatives.

ORDER 9. SYNANDRAE

Five families, viz., Campanulaceae, Goodeniaceae, Candolleaceae, Calyceraceae, and Compositae, are included by Wettstein in the Synandrae.

CAMPANULACEAE

One division of the Campanulaceae, the Lobelioideae, is often separated as a family, Lobeliaceae; and the geographical distribution of the

two divisions, Campanuloideae and Lobelioideae, is quite different. A

milky sap, like that of the Apocynaceae, is present.

The largest genus of the Campanuloideae, Campanula, is essentially a boreal type and is best developed in the mountainous regions of Central Europe. C. rotundifolia is found throughout northern Europe and America as far north as Lapland and Alaska.

The flower in Campanula is actinomorphic and usually bell-shaped; but a common American species, C. americana, has a rotate corolla. The five stamens surround the style and in some species are united. The

inferior ovary has 3-5 chambers.

The family is represented in the Southern Hemisphere by a number of genera, among which is Wahlenbergia, much like Campanula, having numerous species in South Africa and Australia. Many species of Campanula are favorite garden plants, and also the nearly related Platycodon from Japan and China.

The Lobeliaceae are for the most part tropical or subtropical, although some species reach the temperate zones. Lobelia, the largest genus, is cosmopolitan, but is most numerous in the South Temperate regions, especially in South America and South Africa. They are mostly herbaceous plants, but may become shrubs or even small trees. This is especially marked in some Hawaiian species of Lobelia, and several endemic genera, e.g., Cyanea and Clermontia. The Lobeliaceae have more species than any other family in the Hawaiian flora.

There are about a dozen species of Lobelia in the United States, the most striking being the cardinal flower, L. cardinalis, of the Atlantic States and the similar L. splendens from southern California. The brilliant scarlet flowers of these species are probably pollinated by hummingbirds. In the Hawaiian Islands it is said that small honey-sucking birds frequent some of the Lobeliaceae. The strongly zygomorphic corolla of Lobelia is very different from the actinomorphic flowers of Campanula, and the narrow tube is cleft down the inner side. The stamens are united into a tube surrounding the style. The ovary is bilocular.

GOODENIACEAE, CANDOLLEACEAE

These two families are almost exclusively confined to Australia. The Goodeniaceae are evidently related to the Lobeliaceae but do not have the milky latex of the latter, and the flowers have the stamens free. Some of the Goodeniaceae have showy flowers, e.g., Leschenaultia formosa, one of the most beautiful of the many showy flowers of western Australia. The largest genus is Scaevola, and the only one with species outside Australia. S. Lobelia (= S. Koenigii) is a common strand plant throughout the tropics. In Hawaii there are eight species, all but two endemic, and the largest number outside of Australia.

The Candolleaceae, with about one hundred species, are mostly Australian; but the largest genus, *Candollea* (= Stylidium), has a few species in New Zealand and in tropical Asia.

CALYCERACEAE

This small family is found only in South America, mainly in the Andean and subantarctic regions. They are evidently closely related to the Compositae, the flowers being in a dense head, enclosed in bracts, forming an involucre.

COMPOSITAE

Reviewing the Sympetalae, one finds that they do not comprise a homogeneous assemblage and the evolution of the different lines of development has not always followed the same course. Two principal trends may be noted: In some families, e.g., Labiatae, Scrophulariaceae, and other families forming Hutchinson's "Personales," the primitive actinomorphic corolla becomes conspicuously zygomorphic and there are modifications of the stamens and pistil associated with adaptations to insect pollination. In another line, of which the Compositae are the culmination, there is much less modification of the individual flower, but the flowers tend to form a compact inflorescence, a condition which reaches its most complete expression in the Compositae. This "compound" flower has evidently proved its efficiency in the struggle for existence, and the Compositae are notorious for their success in competition with other floral types.

The aggregate type of inflorescence is found also in the Umbelliferales, from which the Rubiales have presumably sprung; and from some of the latter the ancestors of the Compositae probably originated.

In the highly specialized flowers of the Personales, as in the Orchidaceae, pollination is often dependent on specific insects. In the aggregate inflorescence of Umbelliferae or Compositae pollination may be effected by a great variety of insects, so that practically every fertile flower sets seed.

The Compositae are cosmopolitan and it has been estimated that they include about 10 per cent of all the described angiosperms and, except for the Orchidaceae, form the largest family. More than eight hundred genera with over thirteen thousand species have been recorded. The greatest number of species are American, and the Compositae are a very important factor in the floras of both the temperate and tropical parts of both North and South America. There are also many genera and species in all parts of the Old World. Except as aquatics they have held their own under pretty much all ecological conditions.

Owing to their hardiness and the various devices for distributing their

seeds, many species are among the most persistent weeds, and have followed man in his migrations. Many of the commonest weeds, like dandelions, thistles, burdock, and others, are immigrants from Europe.

The majority of the Compositae in the temperate regions are herbaceous, some annuals, others biennial or perennial. In the tropical and subtropical regions are many shrubby species and even some small trees. In the arid regions of the Southwest and in California are shrubby species like the sagebrush (Artemisia), Baccharis, Encelia, Hazardia, Chrysothamnus, and others.

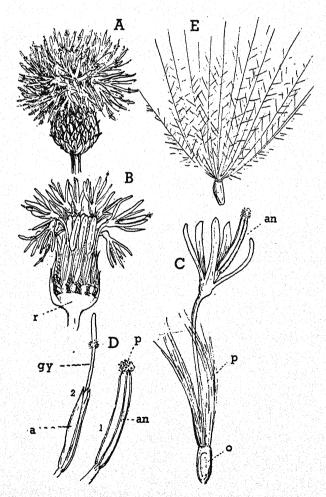


Fig. 350.—Cirsium arvense. C, single flower; p, pappus; o, ovary; an, stamens; E, ripe fruit; showing pappus

The Compositae comprise the largest single element in the flora of the United States. In the Eastern States over one hundred genera occur, and an even larger number in the Pacific States. California alone has over one hundred fifty genera, of which a large number are peculiar to the Pacific Coast.

Floral structure.—The end of the shoot which forms the floral axis is expanded into a broad disc or receptacle, which is often more or less conical. The receptacle with the crowded florets attached forms the head or "capitulum," characteristic of the Compositae. The capitulum is surrounded by a conspicuous, calyx-like involucre composed of numerous imbricated bracts.

All of the flowers of the inflorescence may be alike or there may be two kinds of flowers, the disc florets and the marginal ray flowers. The disc flowers are in most cases hermaphrodite and the tubular corolla is actinomorphic. In the ray flower the corolla is split and flattened and forms the showy rays of the capitulum. The ray flowers are most commonly pistillate, but may be neutral-i.e., the pistil abortive and no seed formed. The five stamens are attached to the tube of the corolla. The filaments are free, but the elongated anthers are united into a tube which encloses the pistil. The pollen is usually discharged before the pistil is mature, and thus cross-pollination is necessary. The pistil then elongates, and the apex in most cases separates into two divergent branches, corresponding to the two carpels of which the pistil is composed. Each branch develops the receptive stigmatic region which receives pollen from a younger flower. The inferior ovary is unilocular, only one carpel being fertile. There is a single basal anatropous ovule. The single seed is fused with the tissue of the ovary, forming the characteristic "achene." The achene is crowned by a circle of scales or fine hairs, sometimes branched. These constitute the pappus, and facilitate the distribution of the achenes. The pappus develops from the margin of the inconspicuous calyx.

The flowers and fruit of the Compositae are most like those of the Dipsacaceae, from which, however, they differ in having "synandrous" stamens; but the structure of the ovary and fruit is much the same. The seed of the Dipsacaceae, however, has a relatively small embryo embedded in endosperm, while the Compositae are "exalbuminous." The Valerianaceae also resemble the Compositae in floral structure, but the number of stamens is reduced and there may be three carpels; but only one is fertile, as in the Compositae, and the seed is also exalbuminous. In both the Dipsacaceae and the Valerianaceae there may be a conspicuous pappus.

Classification.—There are two very distinct main divisions of the Compositae, one in which some or all of the flowers are tubular, the other in which all of the flowers are ligulate, i.e., have a split, strap-shaped

corolla. These have been called Tubuliflorae and Ligulatae, and might be called subfamilies. The latter group, however, differs so much from the Tubuliflorae that it is sometimes removed from the Compositae and regarded as a separate family, Cichoriaceae; and this would seem to be a more natural arrangement.

Ligulatae (Cichoriaceae).—The Ligulatae are much less numerous than the Tubuliflorae, and the majority are confined to the warmer parts of the North Temperate Zone and they are much more abundant in Eurasia than in North America. The Mediterranean countries especially have many genera and species. There are comparatively few in the Southern

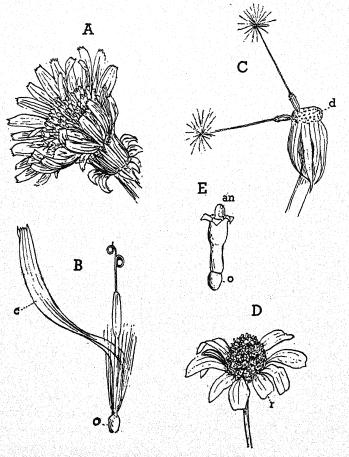


Fig. 351.—A-C, Taraxacum officinalis; B, single flower; C, receptacle, with two fruits attached; D, E, Anthemio Cotula; E, disc flower.

Hemisphere, and in North America most of the endemic forms are found in the Pacific region, especially California, which has about a dozen, mostly small, indigenous genera. Very few indigenous species are found in the Atlantic States, although a good many common weeds like the chicory and dandelion and species of *Lactuca*, *Sonchus*, and *Hieracium* are abundant everywhere.

A common feature of the Ligulatae, in which they differ from all the other Compositae, is the presence of a milky latex, a character they share with the Campanulaceae, with which they may possibly be remotely related.

The flower.—The flowers of the Ligulatae are usually all alike and hermaphrodite. The corolla is ligulate, the apex showing five teeth corresponding to the five petals of which it is composed. The stamens and pistil most nearly resemble those of some of the lower Tubuliflorae, e.g., Vernonieae. In the young flower bud the corolla is tubular, but later splits along one side and assumes the ligulate form. The evident resemblance of the corolla of the Ligulatae to that of the Lobeliaceae and the presence of latex have been cited as indications of relationship. The very great difference in the structure of the ovary, however, makes any near relationship extremely improbable, since the structure of ovary and fruit in the Ligulatae is the same as in the other Compositae.

Tubuliflorae.—The great majority of the Compositae belong to the Tubuliflorae, which have numerous representatives throughout the United States and include many of the showiest and most abundant native flowers, like the goldenrods, asters, sunflowers, and many others. The Pacific Coast, especially California, has many peculiar genera, like the tarweeds (Madia, Hemizonia), Lavia, Coreopsis, Encelia, Gaillardia, etc.

The simplest types of inflorescence are found in Vernonia and Eupatorium, and their relatives. In these the tubular flowers are all alike, the number of florets is small, and they form a loose inflorescence, suggesting that of some of the Rubiales, e.g., Asperula and Valeriana. Occasionally the flowers are dioecious, e.g., in Antennaria and Baccharis, the last a common genus in California. A much larger number of the Tubuliflorae have the two types of flowers—the tubular disc florets, and the ligulate ray florets. The latter may be either pistillate (fertile) or neutral (sterile). The ray florets are usually conspicuously colored. There are some intermediate types between those forms with only disc flowers, e.g., Eupatorium, and those with ray florets. Thus the genus Grindelia has species with and without rays, and in Solidago the rays are few and relatively inconspicuous.

The subfamily Cynareae, to which belong the thistles (Cirsium and Cnicus), the artichoke (Cynara), and the cornflower (Centaurea), is

generally placed at the head of the Compositae. These have all the flowers tubular, but they are often relatively large and brilliantly colored. The flowers are usually all hermaphrodite, but sometimes the marginal ones are sterile. The involucre in the Cynareae is composed of closely overlapping, often spiny, scales.

Relationships of the Compositae.—It may be said that the Compositae are the most successful of all plants in the struggle for existence. Their flowers have retained a relatively primitive structure and are not overspecialized. Perhaps one might say they have not developed individually like the orchids and Personales but have worked co-operatively. The actinomorphic, pentamerous flower points to their relationship with the Rubiales and through them to some simple Choripetalae, perhaps the Umbelliflorales. The development of the embryo sac is reminiscent of such lower Choripetalae as the Ranales, where there is the same tendency to an increased development of the antipodal cells, which in many of the Compositae develop into a conspicuous haustorium.

By the development of the "compound flower," the capitulum, a most perfect device for insuring cross-pollination has been effected; and because of the many methods for the distribution of the seeds and their extraordinary adaptability to pretty much every environment the Compositae have more than held their own in competition with other plants.

The Tubuliflorae, as already indicated, show marked similarities to the Rubiales and might be perhaps an offshoot of the same stock. Whether such notable similarities between the inflorescence and fruits of the Valerianaceae and the Dipsacaceae, and the Tubuliflorae, may be homoplastic rather than truly homologous, cannot of course be definitely answered. Within the Tubuliflorae the progression from such types as Vernonia and Eupatorium, with uniform tubular flowers in a loose head and few involucral bracts, through the Astereae with definite disc and fertile ray florets, to the sunflower type with massive involucre and sterile ray florets is sufficiently evident. The Cynareae (thistles, etc.), generally regarded as the most specialized of the Compositae, probably represent a divergent line of development.

The relationship of the Ligulatae to the other Compositae is not clear. It is through the Ligulatae that a connection of the Compositae with the Lobeliaceae has been suggested. In the presence of the laticiferous tissue the Ligulatae differ from the Tubuliflorae and resemble the Lobeliaceae, whose flowers, also with the split corolla and united stamens, can be compared with the flowers of the Ligulatae. However, the ovary and many-seeded fruit of the Campanulaceae is essentially different from the single achene of the Ligulatae, which in all respects is that of the typical Compositae.

A very extensive study of the evolution of the Compositae has been made by Professor J. Small. He assumes a common ancestor for all the Compositae and believes that this was derived from the Lobeliaceae, the change in the ovary resulting from mutation. Of the existing Compositae he considers the genus *Senecio* as the primitive type from which all the others have been derived. This is based in part on the cosmopolitan distribution of the *Senecio*, whose origin he believes was in the Andean regions of South America.

It is conceivable however that the two main lines of the Compositae have originated independently—the Tubuliflorae from the Rubiales, the Ligulatae from Campanulales—but it must be confessed that there are

serious objections to this theory.

Very little is known of the geological history of the Compositae, perhaps owing to their predominantly herbaceous habit. Achenes assumed to belong to Compositae have occasionally been preserved as fossils, the oldest-known coming from Lower Eocene rocks. The record is too incomplete, however, to throw much light on their history.

RELATIONSHIPS OF SYMPETALAE

The Sympetalae, the most numerous and specialized members of the dicotyledons, represent the culmination of the angiosperms. It is obvious that sympetaly has developed independently in several unrelated phyla and does not necessarily indicate genetic relationship. As might be expected there is by no means general agreement as to the relationships of the different orders of the Sympetalae and as to their relationship with their choripetalous ancestors; it is therefore impossible, at present, to reach a definitive classification.

Bessey, whose system has been followed to some extent by Hutchinson, derives all of the angiosperms from the Ranales. Of the dicotyledons he recognizes two main lines of development, the Calyciflorae, leading through the Umbellulales and the Rubiales to the Compositae; from the second series, Thalamiflorae, through the Caryophyllales (Centrospermae), all the other sympetalous orders have been derived.

Wettstein, on the other hand, believes that the dicotyledons represent several quite independent phyla and cannot be traced back to a single ancestral type, i.e., they are polyphyletic. He assumes that of the Isocarpae (Bessey's Heteromerae) the Primulales alone were derived from the Centrospermae and are not related to the other Sympetalae; and this is the case also in the other Isocarpae. Of these, Wettstein derives the Ericales from the Guttiferales. Hutchinson connects them with the Theales.

The Diospyrales (Ebenales) are very old types, the genus *Diospyros* occurring in the Cretaceous. Hutchinson derives the Diospyraceae from

the Anonaceae, also a very old family; and this seems more plausible than a relationship with the Centrospermae.

The two orders of Engler, viz., Contortae and Tubiflorae, are united by Bessey into the "Bicarpellatae." This includes four suborders, viz., Polemoniales, Gentianales, Personales, and Lamiales. Of these the Gentianales correspond to the Contortae; the others are subdivisions of the Tubiflorae.

The lowest family of the Contortae, the Oleaceae, is sometimes made the type of an order, Ligustrales. This includes some genera almost or quite dialypetalous, e.g., Fraxinus, which perhaps are distantly related to the choripetalous Celastrales. Some of the genera, like Gentiana and Gelsemium, resemble the Tubiflorae and suggest a possible derivation from some of these. The most specialized families, the Apocynaceae and the Asclepiadaceae, are distinguished by the presence of a milky latex. In the latter family the flowers, while retaining the primitive actinomorphic form, in many genera show extraordinarily complex devices for insect pollination and may be regarded as the most specialized members of the Contortae.

Whether the Tubiflorae are to be regarded as an offshoot of the Contortae or vice versa might be a question for consideration. Engler's large order, Tubiflorae, is a somewhat heterogeneous one and the division into the three suborders proposed by Bessey is probably justified. The lower families of the order, e.g., Convolvulaceae and Polemoniaceae, have strictly actinomorphic flowers, and the Convolvulaceae are usually placed at the base of the Tubuliflorae. Peter, who treats this family in the Natürlichen Pflanzenfamilien, considers the Convolvulaceae as the central type of the Tubiflorae, from which the other families diverge. The Solanaceae are intermediate in character between the strictly actinomorphic Convolvulaceae and the Personales. While most of the Solanaceae have the typical actinomorphic flowers, a few genera, like Salpiglossis and Schizanthus, have a definitely zygomorphic corolla and only four functional stamens.

Bessey places in the Personales eight families, of which the most important are Scrophulariaceae, Bignoniaceae, and Acanthaceae. The flowers of the Personales are the most specialized of any of the Sympetalae and culminate in such families as the Scrophulariaceae and the Bignoniaceae, which represent the most highly developed floral types among the dicotyledons. The Personales also include such specialized families as the parasitic Orobanchaceae and the aquatic bladderweeds (*Utricularia*), with their extraordinary complex traps for the capture of minute aquatic organisms.

In the Borraginaceae the tendency toward zygomorphy has been re-

ferred to; and this, together with the four free nutlets or achenes, suggests a possible approach to the Verbenaceae and the Labiatae, the latter especially with pronounced zygomorphy and 2—4 stamens. These two families constitute Bessey's Lamiales, of which the Labiatae may be said to close the direct line of evolution in the Bicarpellatae. Bessey considers the Gentianales (Contortae) and the Personales as side branches of this main line of development, the end members of which are the Lamiales.

The Rubiales evidently have had an origin quite independent from that of the Tubiflorae and the Contortae and it is generally believed are related to the Umbelliferales, these, according to Bessey, belonging to the Calyciflorae. Of the Umbelliflorae, the Cornaceae perhaps are nearest the Rubiales. The Rubiales have epigynous flowers and with the Campanulatae are included by Bessey in his third order of Sympetalae—Inferae—distinguished from the other Sympetalae by the inferior ovary.

In the Engler system the Rubiales include five families. Bessey restricts the suborder to two families, Rubiaceae and Caprifoliaceae, and removes the Valerianaceae and Dipsacaceae to a special suborder Asterales, with

the Compositae ending the series.

The flowers of the Valerianaceae and the Dipsacaceae resemble still more those of the Compositae and might possibly be regarded as connecting the Rubiales and the Compositae, although this of course is by no means certain. The flowers of the Compositae, however, differ greatly in the character of the stamens. In the Valerianaceae and the Dipsacaceae the stamens are reduced in number and are entirely free, while the five stamens of the Compositae have the anthers united. The fruit of the two families is an achene, sometimes with a "pappus," and closely resembles the achene of the Compositae. In the Dipsacaceae the compact inflorescence surrounded by a conspicuous involucre is comparable to the capitulum of the Compositae. In Scabiosa the resemblance is increased by the presence of two types of florets, the outer ones being greatly enlarged, recalling the ray florets of a composite capitulum.

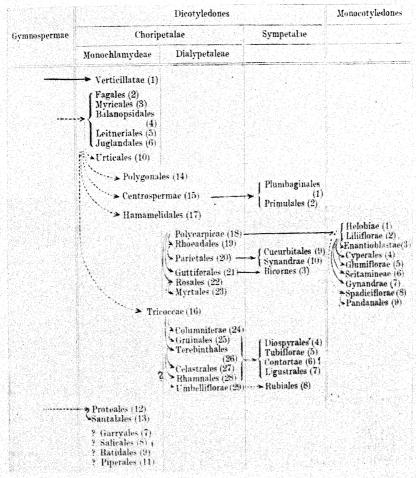
While it can hardly be maintained that the sequence Rubiaceae—Valerianaceae—Dipsacaceae leads directly to the Compositae, this sequence would seem to indicate the possibility that the Tubuliflorae, at least, have

been derived from the same stock as the Rubiales.

The question of the origin of the Ligulatae (Cichoriaceae) is a puzzling one. Their obvious resemblances to the Lobeliaceae, viz., the split corolla, synandrous stamens, and the presence of latex, point to a real relationship between the two families. There is, however, the very marked difference in the characters of the ovary and fruit, which in the Cichoriaceae are the same as in the typical Compositae. However, the two families Goodeniaceae and Candolleaceae, related to the Lobeliaceae, are to

some extent intermediate as to the ovary between the Lobeliaceae and Cichoriaceae.

Bessey considers the Campanales (which includes the Lobeliaceae) as a branch of the same stock, Rubiales, which culminates in the Compositae. Should the Cichoriaceae be the end of this lateral branch, their resemblances to the other Compositae would not imply a direct relationship but would be homoplastic.



Phylogeny of the Angiosperms, after Wettstein

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